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NOAA Technical Report NMFS 42 September 1986

# Effects of Temperature on the Biology of the Northern Shrimp, *Pandalus borealis*, in the Gulf of Maine

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# Effects of Temperature on the Biology of the Northern Shrimp, *Pandalus borealis*, in the Gulf of Maine

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## ABSTRACT

**Length-frequency data collected from inshore and offshore locations in the Gulf of Maine in 1966-1968 indicated that ovigerous female northern shrimp (*Pandalus borealis*) first appeared offshore in August and September and migrated inshore in the fall and winter. Once eggs hatched, surviving females returned offshore. Juveniles and males migrated offshore during their first two years of life. Sex transition occurred in both inshore and offshore waters, but most males changed sex offshore during their third and fourth years. Most shrimp changed sex and matured as females for the first time in their fourth year. Smaller females and females exposed to colder bottom temperatures spawned first. The incidence of egg parasitism peaked in January and was higher for shrimp exposed to warmer bottom temperatures. Accelerated growth at higher temperatures appeared to result in earlier or more rapid sex transition. Males and non-ovigerous females were observed to make diurnal vertical migrations, but were not found in near-surface waters where the temperature exceeded 6°C. Ovigerous females fed more heavily on benthic molluscs in inshore waters in the winter, presumably because the egg masses they were carrying prevented them from migrating vertically at night.**

**Northern shrimp were more abundant in the southwestern region of the Gulf of Maine where bottom temperatures remain low throughout the year. Bottom trawl catch rates were highest in Jeffreys Basin where bottom temperatures were lower than at any other sampling location. Catch rates throughout the study area were inversely related to bottom temperature and reached a maximum at 3°C.**

**An increase of 40% in fecundity between 1973 and 1979 was associated with a decline of 2-3°C in April-July offshore bottom temperatures. Furthermore, a decrease in mean fecundity per 25 mm female between 1965 and 1970 was linearly related to reduced landings between 1969 and 1974. It is hypothesized that temperature-induced changes in fecundity and, possibly, in the extent of egg mortality due to parasitism, may provide a mechanism which could partially account for changes in the size of the Gulf of Maine northern shrimp population during the last thirty years.**

## INTRODUCTION

The northern or pink shrimp, *Pandalus borealis* Krøyer, supports sizeable otter trawl fisheries throughout much of its range within boreal and sub-arctic waters of the northern hemisphere. In 1980, a total world catch of 164,000 metric tons (mt) of pandalid shrimp was reported, of which 35% came from the northeast Atlantic, 25% from the northwest Atlantic, and 27% from the northeast Pacific (FAO 1981). Total world catch doubled between 1970 and 1980 and increased by 19% between 1979 and 1980 (FAO 1976, 1981). Major pandalid shrimp fisheries (60% *P. borealis* in 1980) are conducted on the west coast of North America from California to Alaska, in the Canadian maritime provinces, on the west coast of Greenland, and in the Norwegian and North Seas (Balsiger 1981).

In the Atlantic, *P. borealis* reaches its southernmost limit in the Gulf of Maine where it has supported a commercial fishery of some importance for the last four decades. Historically, the Gulf of Maine shrimp fishery has been characterized by marked variations in annual landings. In the first 17 years after statistics were first systematically recorded (1938), landings were modest and reached a maximum of 255 mt in 1945 (Fig. 1), but declined thereafter. No landings were recorded during 1954-57, even though fishermen continued to look for shrimp. The fishery revived in 1958 and, beginning in 1962, landings increased dramatically every year, reaching a peak of 12,800 mt in 1969 (Table 1). Maine fishermen accounted for nearly all landings in the Gulf during 1940-68 and for 72% of total landings during the height of the fishery (1966-75). Maine landings peaked at 10,990 mt in 1969 (Fig. 2). Harvesting efforts in Maine have traditionally been directed at the capture of egg-bearing females which migrate inshore in the winter. Massachusetts fishermen began harvesting shrimp on a large scale in inshore and offshore waters in 1969. A gradual decline in landings which began after 1972 accelerated rapidly in the mid-1970s; less than 1000 mt a year were landed in 1977, 1979, and 1980. (The fishery was closed completely by regulation in 1978.) Catches exceeded 1000 mt per year after 1980, reaching 3900 mt in the winter of 1984-85 (Table 1).

Examination of catch, catch-per-unit-effort (CPUE), and annual mean sea-surface temperatures during the period of rapid growth and decline of the fishery (Fig. 3) indicate that increased catches in the late 1960s were preceded by a rapid increase in population

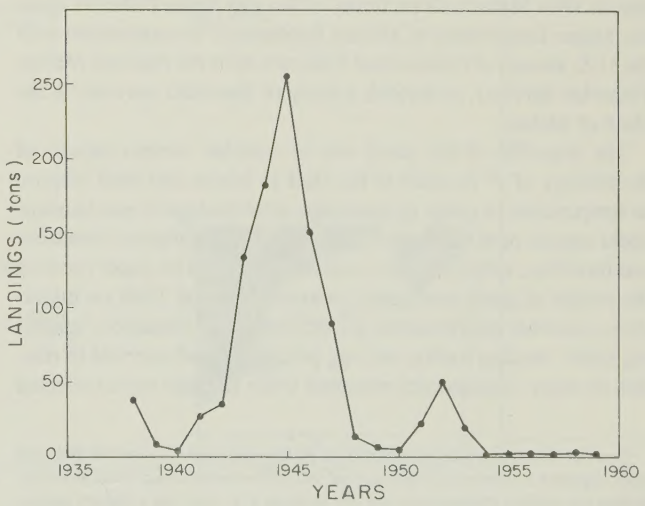


**Figure 1.—Annual Maine landings of *Pandalus borealis*, 1938-59.**

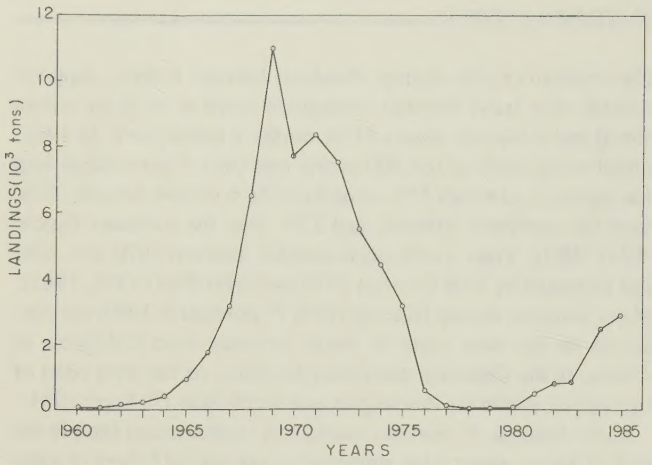


**Figure 2.—Annual Maine landings of *Pandalus borealis*, 1960-85.**

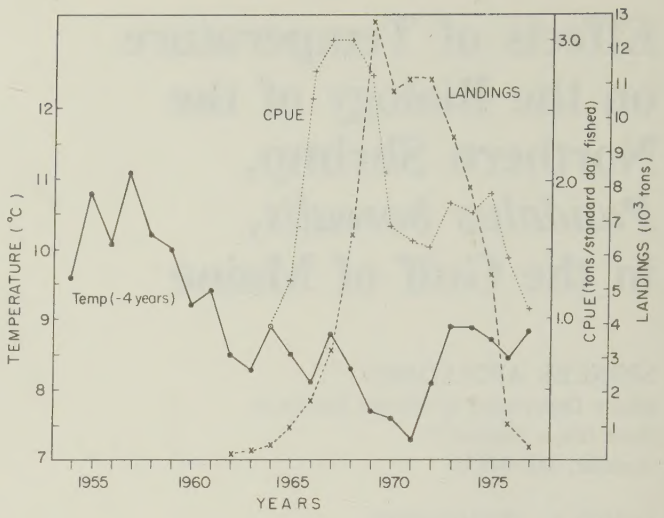


**Figure 3.—Mean annual 1950-73 sea surface temperatures (lagged 4 years) at Boothbay Harbor, Maine, total 1962-77 catch, and 1964-77 catch-per-unit-effort (CPUE) data estimated from commercial landings of 34-50 GT vessels in Gloucester and Portland for which shrimp accounted for 50% or more of the catch. *Sources*: Temperature data from Welch and Churchill (1985); catch and CPUE data from Schick et al. (1981).**

size (as inferred from CPUE data). Catch remained high from 1969 to 1972 despite a fairly dramatic reduction in population size. The rapid increase in population size in the mid-1960s was preceded by a drop of 3°C in mean annual sea surface temperatures in the late 1950s. The relation of these three variables after 1969 is not quite so clear, but the implication is that both fishing pressure and temperature changes may affect population size.

Dow (1977) reported a significant negative correlation between annual mean surface temperatures at Boothbay Harbor, Maine, and the log of shrimp landings 4 years later for the period 1939-67[1]. Earlier attempts by Dow (1963, 1964, 1966) to forecast shrimp landings in the Gulf of Maine were based on an assumed 2-year lag between spawning and exploitation, according to length-at-age information reported by Rasmussen (1953) for *P. borealis* in Norway. He was handicapped, however, by the lack of specific biological data for the Gulf of Maine population, particularly the age-at-maturity and the age-at-first-capture. It was to provide specific information on life history characteristics, to relate them if possible to changes in temperature, and to provide a sound biological basis for managing the increasingly valuable winter shrimp fishery, that in 1966 Maine's Department of Sea and Shore Fisheries (now the Maine Department of Marine Resources), in cooperation with the U.S. Bureau of Commercial Fisheries (now the National Marine Fisheries Service), undertook a study of *Pandalus borealis* in the Gulf of Maine.

The objective of this study was to examine various aspects of the biology of *P. borealis* in the Gulf of Maine and their relation to temperature in order to determine what biological mechanisms could explain how temperature changes affect population abundance and therefore, indirectly, the commercial catch. This paper presents the results of work conducted between 1966 and 1968 on migrations, seasonal distributions, growth rates, sex transition, spawning times, feeding habits, and egg production and survival in relation to water temperatures recorded when samples were collected

[1]Dow, in subsequent articles published in *Fishing News International* in 1981 and 1985, reported a correlation coefficient of −0.950 between annual mean Boothbay Harbor sea surface temperatures and log landings 4 yr later for a shorter period, 1949-68. It was not stated whether or not this strong negative correlation was statistically significant.

**Table 1.—Commercial landings (metric tons) of northern shrimp in the Gulf of Maine, by state, 1958-85.**

| Year | Maine | N.H. | Mass. | Total |
|---|---|---|---|---|
| 1958 | 2 | — | 0 | 2 |
| 1959 | 5 | — | 2 | 8 |
| 1960 | 40 | — | 1 | 41 |
| 1961 | 30 | — | 1 | 31 |
| 1962 | 160 | — | 16 | 176 |
| 1963 | 244 | — | 10 | 254 |
| 1964 | 419 | — | 3 | 423 |
| 1965 | 947 | — | 8 | 955 |
| 1966 | 1,738 | 18 | 11 | 1,766 |
| 1967 | 3,141 | 20 | 10 | 3,171 |
| 1968 | 6,515 | 43 | 52 | 6,610 |
| 1969 | 10,993 | 58 | 1,773 | 12,824 |
| 1970 | 7,713 | 54 | 2,902 | 10,670 |
| 1971 | 8,355 | 51 | 2,724 | 11,129 |
| 1972 | 7,516 | 75 | 3,505 | 11,095 |
| 1973 | 5,477 | 60 | 3,868 | 9,405 |
| 1974 | 4,431 | 37 | 3,477 | 7,945 |
| 1975 | 3,177 | 30 | 2,080 | 5,287 |
| 1976 | 617 | 7 | 398 | 1,022 |
| 1977 | 148 | 2 | 237 | 387 |
| 1978 | — | — | — | — |
| 1979 | 33 | 2 | 451 | 487 |
| 1980 | 70 | 5 | 257 | 332 |
| 1981 | 529 | 5 | 538 | 1,071 |
| 1982[a] | 853 | 22 | 659 | 1,531 |
| 1983[a] | 892 | 46 | 460 | 1,399 |
| 1984[ab] | 2,395 | 31 | 525 | 2,951 |
| 1985[ab] | 2,946 | 216 | 968 | 4,131 |

Source: Diodati et al. (1985).

[a]Landings computed on a seasonal basis, e.g., 1982 includes December 1981, but not December 1982.

[b]Preliminary estimates.

and to long-term trends in monthly and annual sea surface and bottom temperatures. Considerable emphasis was placed on the interrelationship between temperature and migrations, since migratory behavior was believed to be a reproductive strategy with important management implications.

Previous studies of the biology and ecology of *P. borealis* have been conducted by a number of workers: Wollebaek (1903) and Hjort and Ruud (1938) in Norway, Rasmussen (1953) from southern Norway to Spitsbergen, Horsted and Smidt (1956) in Greenland, Allen (1959) in the North Sea, Butler (1964) in British Columbia, and Haynes and Wigley (1969) in the Gulf of Maine. Reviews have been published by Butler (1971), Balsiger (1981), and, most recently, by Shumway et al. (1985).

## METHODS

Sampling from the chartered vessel *Draggin Lady* began in the early summer of 1966 in inshore waters and on a few offshore grounds such as Jordan Basin and Jeffreys Basin (see Table 2 and Figure 4). In the winter of 1966-67, stations 1 and 2 were sampled twice a month and both sides of Jeffreys Ledge (stations 5 and 6) were sampled once in midwinter. In the summer of 1967, a larger number of offshore areas were sampled several times. As the work progressed, it became obvious that more extensive and more frequent sampling was necessary. Therefore, in the winter of 1967-68, sampling was carried out approximately once a month as weather permitted at stations 1-6: two additional samples were collected at station 7. In the summer of 1968 the same schedule was continued at stations 1-6, and stations 7-12 were added to the monthly program. This expanded sampling program was carried out from June

**Table 2.—Sampling locations for *Pandalus borealis* in the Gulf of Maine, 1966-68.**

| Station no. | Location | Depth (m) | Latitude | Longitude |
|---|---|---|---|---|
| 1 | Cuckolds Light | 60 | 43° 45′ | 69° 39′ |
| 2 | 10 miles south of Boothbay Harbor | 128 | 43° 34′ | 69° 35′ |
| 3 | 20 miles south of Boothbay Harbor | 165 | 43° 26′ | 69° 32′ |
| 4 | West of Platts Bank | 178 | 43° 09′ | 69° 55′ |
| 5 | West of Jeffreys Ledge | 165 | 43° 03′ | 70° 11′ |
| 6 | East of Jeffreys Ledge | 211 | 43° 02′ | 69° 55′ |
| 7 | East of Three Dory Ridge | 188 | 43° 10′ | 69° 13′ |
| 8 | West of Fippennies Ledge | 180 | 42° 44′ | 69° 31′ |
| 9 | West of Cashes Ledge | 192 | 42° 57′ | 69° 02′ |
| 10 | Northeast of Cashes Ledge | 183 | 43° 03′ | 68° 53′ |
| 11 | 20 miles south of Mt. Desert Rock | 174 | 43° 37′ | 68° 03′ |
| 12 | 23 miles southeast of Mt. Desert Rock | 240 | 43° 38′ | 67° 51′ |

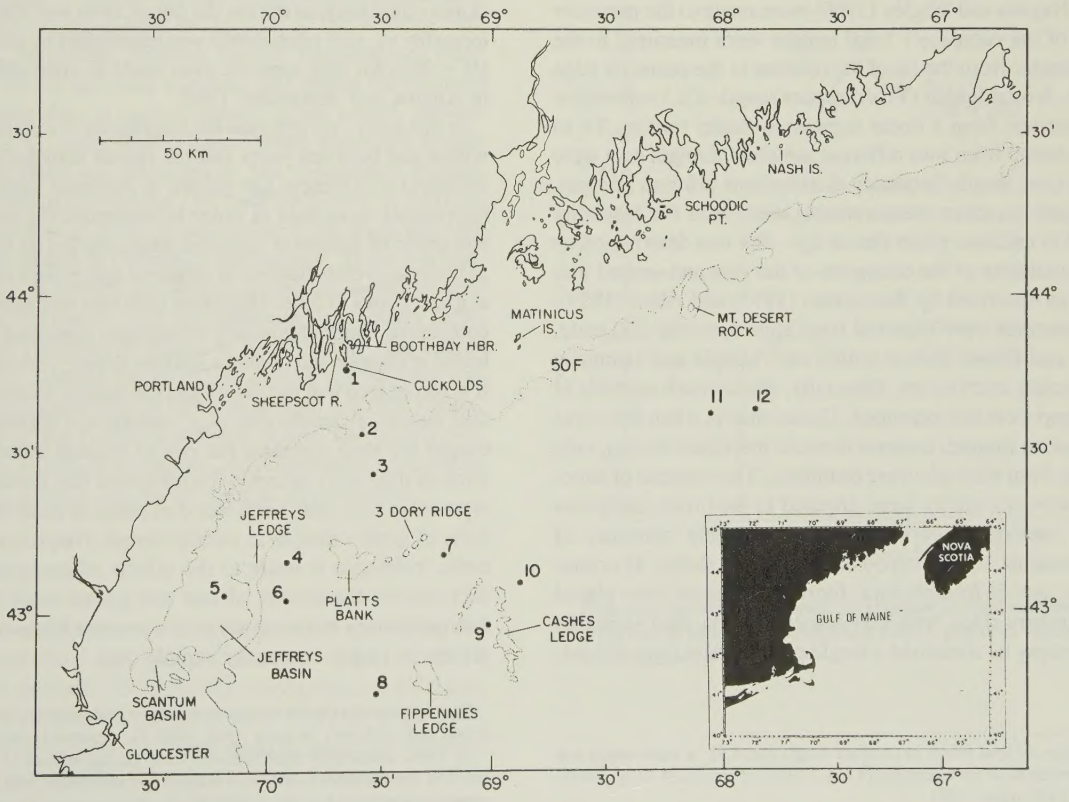


**Figure 4.—Shrimp sampling locations in the Gulf of Maine in 1966-68 (see Table 2).**

through September 1968. Occasionally, supplementary samples were taken by the *Draggin Lady* in other inshore and offshore areas or from commercial catches by Boothbay Harbor fishermen. (Commercial catches were sampled only to estimate the percentage frequency of normal and parasitized eggs carried by female shrimp.) Beginning in the spring of 1967, continuous vertical temperature recordings were made with a bathythermograph at each station except Cuckolds each time a sample was collected. The U.S. Bureau of Commercial Fisheries made frequent measurements at Cuckolds and, through the courtesy of Dr. J. J. Graham, those data were used in this study.

All shrimp samples aboard the *Draggin Lady* were collected using a semiballoon otter trawl with a 7.6 m (25 ft) head rope and 9.4 m (31 ft) foot rope, with 38 mm (1.5 in) mesh in the body, and a cod end with 32 mm (1.25 in) mesh covered with a 13 mm (0.5 in) mesh liner. The net was fished from a single wire with 92 m (100 ft) bridles. Towing speed was approximately 2 knots and all tows lasted approximately 30 minutes. When catches were large, four subsamples of about 100-125 shrimp were collected at random from the entire catch as it lay on the deck, preserved in 5% formalin, and returned to the laboratory for analysis. For small catches, all shrimp were saved. Total catches were recorded only as estimated volume, not as numbers or weight.

Vertical migratory behavior was studied by deploying baited shrimp pots at different depths. Successful experiments were conducted in Jeffreys Basin in August 1967, in the Sheepscot River in March 1968, and at the 20-mile station in May and July 1968. In each case, pots were hauled periodically and the contents of each pot removed, sexed, and counted. The pots used were the same design as those described by McBride and Barr (1967).

Shrimp were measured to the nearest 0.1 mm from the posterior edge of the eye socket to the extreme posterior lateral edge of the carapace in the manner of Horsted and Smidt (1956) and Allen (1959). (Measurements reported by Rasmussen (1953), Butler (1964), and Haynes and Wigley (1969) were made to the posterior dorsal edge of the carapace.) Total lengths were measured to the nearest millimeter from the tip of the rostrum to the posterior edge of the telson. A total length (TL)/carapace length (CL) conversion factor was derived from a linear regression model relating TL to CL for 486 shrimp from four different samples[2]. Length data were compiled as total length frequency distributions (10 mm groups), but the original carapace measurements were used for fecundity analyses and to estimate mean size-at-age. Sex was determined by noting the conditions of the endopods of the first and second pair of pleopods as described by Rasmussen (1953) and Allen (1959).

Stomach contents were removed from approximately 200 male, transitional, and female shrimp within each sample and examined under a dissecting microscope. Generally, the stomach contents of 0-group shrimp were not examined. Occasionally, when there was little difference in stomach contents between individual shrimp, only 100 stomachs from a sample were examined. The contents of stomachs which were not empty were grouped in the broad categories of 1) mud, including debris and unrecognizable material, 2) polychaete remains, 3) pelycypod and gastropod shells, 4) crustacean remains, and 5) foraminifera. Individual shrimp were placed in a single category since, with very few exceptions, their stomachs were either empty or contained a single predominant type of food.

In order to describe size increments in general terms which ignored possible spatial or temporal variations in growth rates, we selected from each calendar month when samples were collected, regardless of the year or sampling location, the length frequency data which showed the most distinct, readily-separable size group or groups. Mean lengths for each identifiable size group were calculated from length frequency data, and mean, maximum, and minimum lengths for each size group were plotted as a function of the presumed age of the size group. The same approach was used by Haynes and Wigley (1969). For size groups which overlapped at intermediate lengths, half of the number of length measurements in the intermediate length class were assigned to each adjacent size group. Age determinations were based on an assumed 1 March birth date[3]. It was further assumed that each clearly defined size group was composed of only one age group, and, since *P. borealis* reproduces once a year, that each of these age groups represented a year-class. (All references to the age of size groups in this report will be to age groups, i.e., 0-group, 1-group, etc.). In order to avoid problems caused by the overlap between older size groups, growth was estimated only for shrimp in their first 3 years of life. No attempt was made to fit a growth curve to mean length-at-age data.

For fecundity studies, all eggs were removed from each ovigerous female and weighed. Eggs collected in 1966 were weighed fresh while those collected in 1968 were preserved in 5% formalin before weighing. For each set of annual data, total egg weights were converted to total egg numbers by means of a linear regression equation which related egg number to egg weight for subsamples from individual egg masses removed from females collected at different locations and sampling dates during August and/or September of each year[4]. Estimated total egg numbers were verified by directly counting all the eggs from a few females and comparing those counts with total estimated egg counts. Allen's (1963) criteria were used to describe stages of egg development. Size-specific fecundity was estimated for shrimp collected during individual sampling occasions at individual stations during the fall of 1966 and 1968. A composite fecundity vs. size relationship was established by combining all data ($N = 202$) for nine separate tows made in eight different locations in August and September 1968.

In this study, we describe the migrations of individual age groups within and between years and the spatial distribution (inshore vs. offshore) of different age groups at different times of year. Both approaches were used in order to determine the movements of an age group of shrimp at different stages during its life cycle as well as the spatial distributions of different age groups in the population at given points in time. Migratory behavior was inferred by visually comparing length frequency histograms compiled from data collected at inshore and offshore stations during various times of year. It is recognized that the use of percent sample frequency data rather than numerical density data (e.g., numbers of shrimp per size group caught per tow) increases the risk of making incorrect interpretations of migratory activity. To minimize this problem, the results reported in this study were based as much as possible on interpretations of gross changes in sample length frequency data. In some cases, reference is made to the effects of presumed increases or decreases in the density of one size group (such as would result from migratory movements) on the percent frequency of other size groups in length frequency sample data.

[2]The ratio (slope) of total length to carapace length was 4.95, a value which was intermediate between those for Greenland (4.6-4.7, Horsted and Smidt 1956) and for the North Sea (5.05, Allen 1959).

[3]This birthdate was based on annual surveys of shrimp larvae in the Sheepscot River during early February to early April, 1978-82, reported in Stickney (1982).

[4]In 1968, subsamples were removed from the egg masses of 24 individuals collected in five different locations in August and September, and a statistically linear regression equation ($Y = 367 + 1037\,X$) was derived where $X$ equals weight in grams.

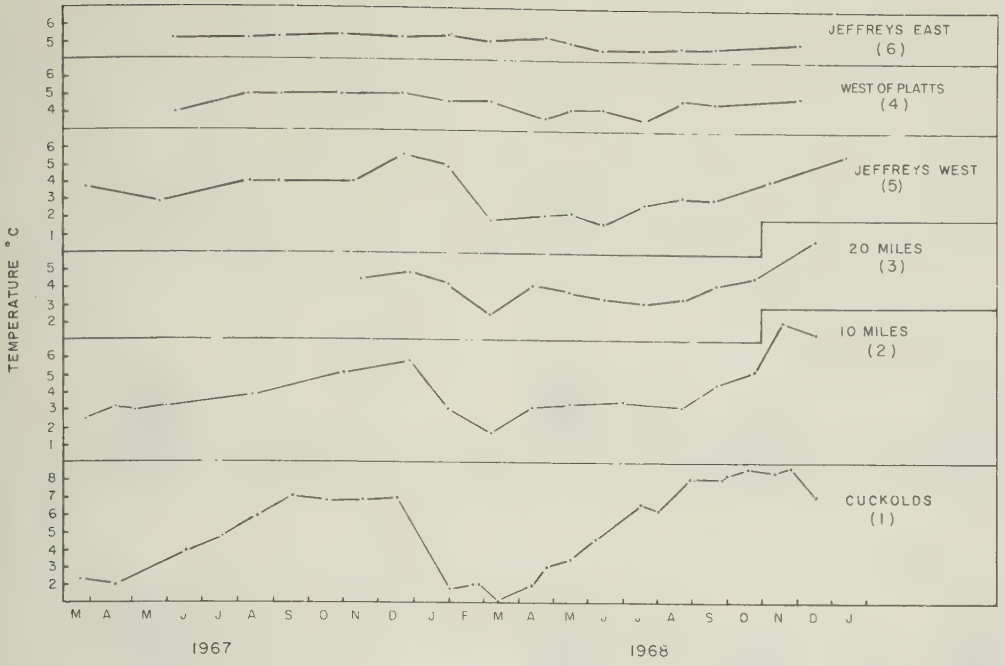


**Figure 5.—Annual variations in bottom temperature at certain sampling locations in the Gulf of Maine, 1967-68 (see Table 2, Figure 4). Station numbers in parentheses.**

## RESULTS

### Temperature measurements

Bottom temperature data collected during this study (Fig. 5) showed a larger annual variation for inshore coastal waters than for offshore locations. Furthermore, inshore bottom temperatures more closely reflected seasonal changes than did the offshore temperatures which lagged behind the calendar seasons by about 5 months. In general, the annual variation in bottom temperatures decreased and the maximum occurred later in the year as the distance offshore increased. Minimum offshore bottom temperatures were recorded in late spring and early summer, and during the summer were 2°-3°C colder than in inshore waters. In the winter, inshore waters were 2°-3°C colder than offshore water where the annual maximum temperature was recorded in late December. Bottom temperatures recorded throughout 1967 and 1968 west of Jeffreys Ledge were lower than at offshore stations on Platts Bank and east of Jeffreys Ledge, except in December and January. There was considerable variation in surface and bottom temperatures, the degree of temperature stratification, and the minimum temperature depth between different sampling locations in the Gulf (see, for example, Figure 6). The greatest degree of temperature stratification was recorded in August each year in the area around Jeffreys Ledge, particularly west of the Ledge in Jeffreys Basin. The lowest bottom temperatures recorded during this study generally occurred at stations with the greatest degree of thermal stratification.

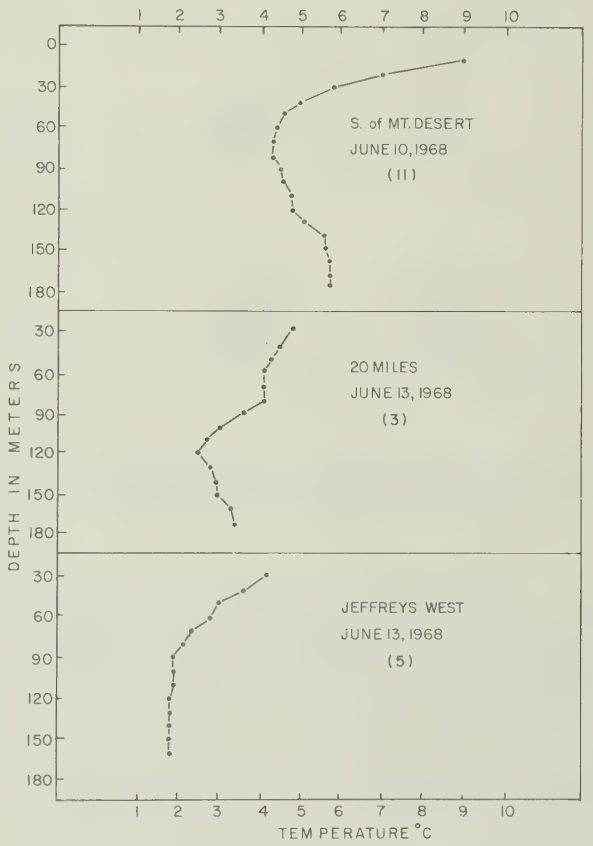


**Figure 6.—Vertical temperature distributions at three sampling locations in the Gulf of Maine in June 1968 (see Table 2, Figure 4). Station numbers in parentheses.**

### Migrations

**Inshore-offshore migrations**—It is convenient, in describing the migrations of individual age groups, to begin in the winter of 1967-68 with the smallest (30-50 mm TL) size group which represented 40-45% of the catch at Cuckolds and 5% or less of the catch in the offshore locations (Fig. 7). These small shrimp were assumed to be a 0-group shrimp which hatched the previous spring (1967 year class). A few 0-group shrimp belonging to the 1967 year class

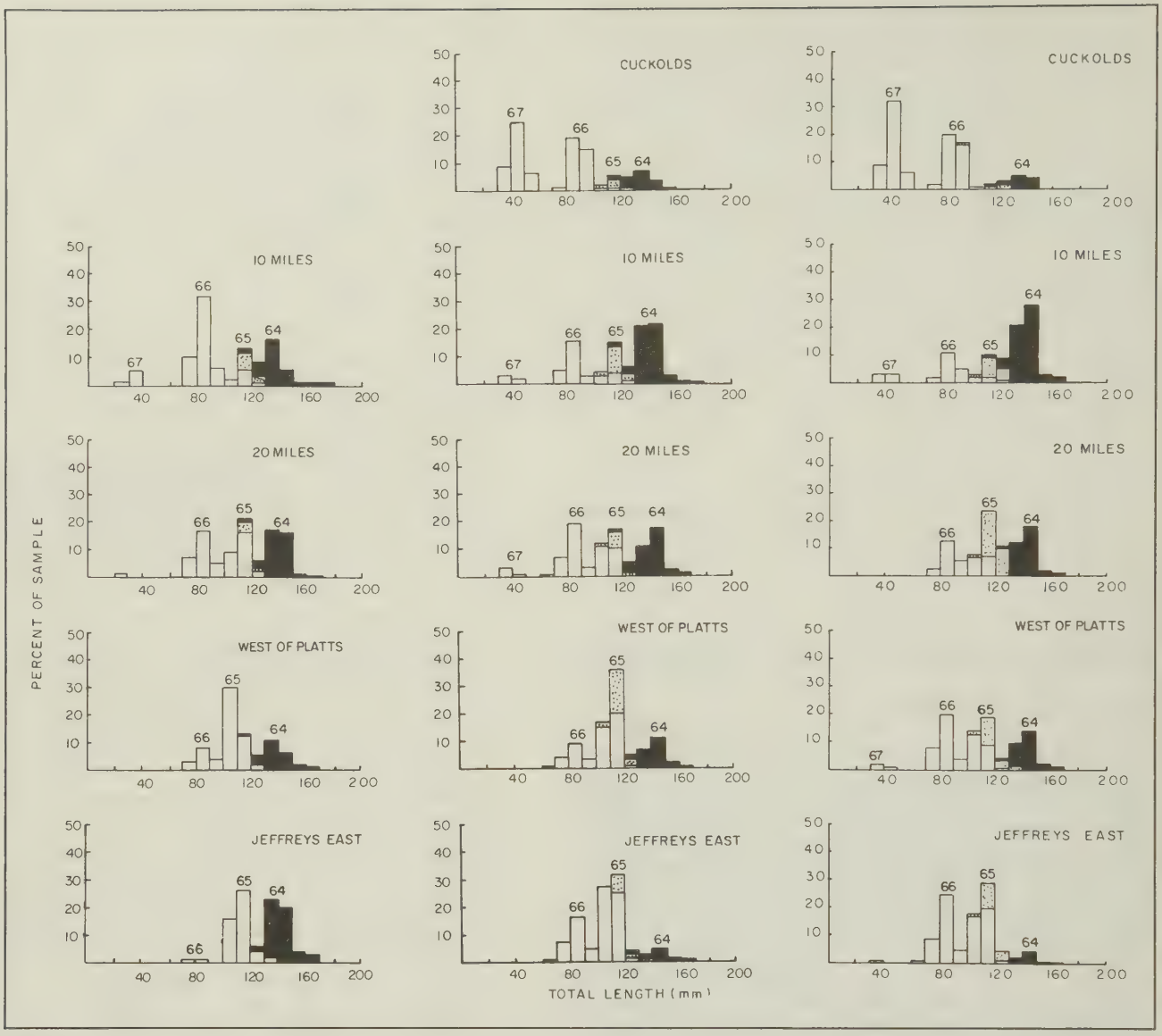


**Figure 7.—Length frequency distributions for *Pandalus borealis* sampled at inshore and offshore locations in the Gulf of Maine: from left to right, 30 Oct.-14 Nov. 1967, 21-27 Dec. 1967, and 31 Jan.-1 Feb. 1968. 1963-67 year classes are labeled in cases where they were clearly identifiable. White = juveniles and males; stippled = transitionals; black = females.**

moved offshore during their first year, appearing at the 20-mile station in November and late December and between Platts Bank and Jeffreys Ledge (stations 4 and 6) in early February. These results clearly indicated that most 0-group shrimp remain within 20 miles of the coast. The presence of a few 0-group shrimp at stations 4 and 6 in early February (Fig. 7) indicated that some shrimp migrate as far as 40 miles offshore during their first year.

The offshore migration of small juvenile and male shrimp which begins during an age group's first year of life continues during its second year. The 1967 year class accounted for a rapidly growing proportion of the inshore samples collected in the spring of 1968; it included 70% of all shrimp collected at Cuckolds in March and May and >95% in June (Fig. 8). (The increasing percentage of 0-group shrimp in the samples collected later in the 1967-68 sampling period undoubtedly reflected their increasing retention in the half-inch mesh sampling gear.) Inshore samples collected in the summers of 1966 and 1967 were composed almost entirely of 1-group shrimp (Fig. 9). Evidence for an offshore migration of 1-group shrimp was provided by length frequency data collected during the summers of 1967 and 1968 (Figs. 10, 11) and the winter of 1967-68 (Fig. 7). These data showed that 1-group shrimp (50-80 mm TL) accounted for up to 25% of the offshore summer samples, but were generally <10%. Percentages of 1-group males (70-90 mm TL) were higher in offshore samples collected in the winter of 1967, reaching 15-35%, and reflected their increasing displacement from inshore to offshore waters as well as the inshore migration of ovigerous females. Shrimp belonging to the 1966 year class remained at Cuckolds through May of their second year, but were almost gone by June (Fig. 7).

Based on the above information alone, one would conclude that the offshore migration of males (and juveniles), which begins in an age group's first year, is completed by its third summer. Interpretation of length frequency data for the older age groups, however, casts doubt on this conclusion. Shrimp belonging to the 1965 year class were present as 2 and 3-group shrimp at most inshore and offshore sampling locations during the 1967-68 sampling season (Figs. 7, 8) and at offshore stations during the summers of 1967 and 1968 (Figs. 10, 11). On some occasions, however, this year

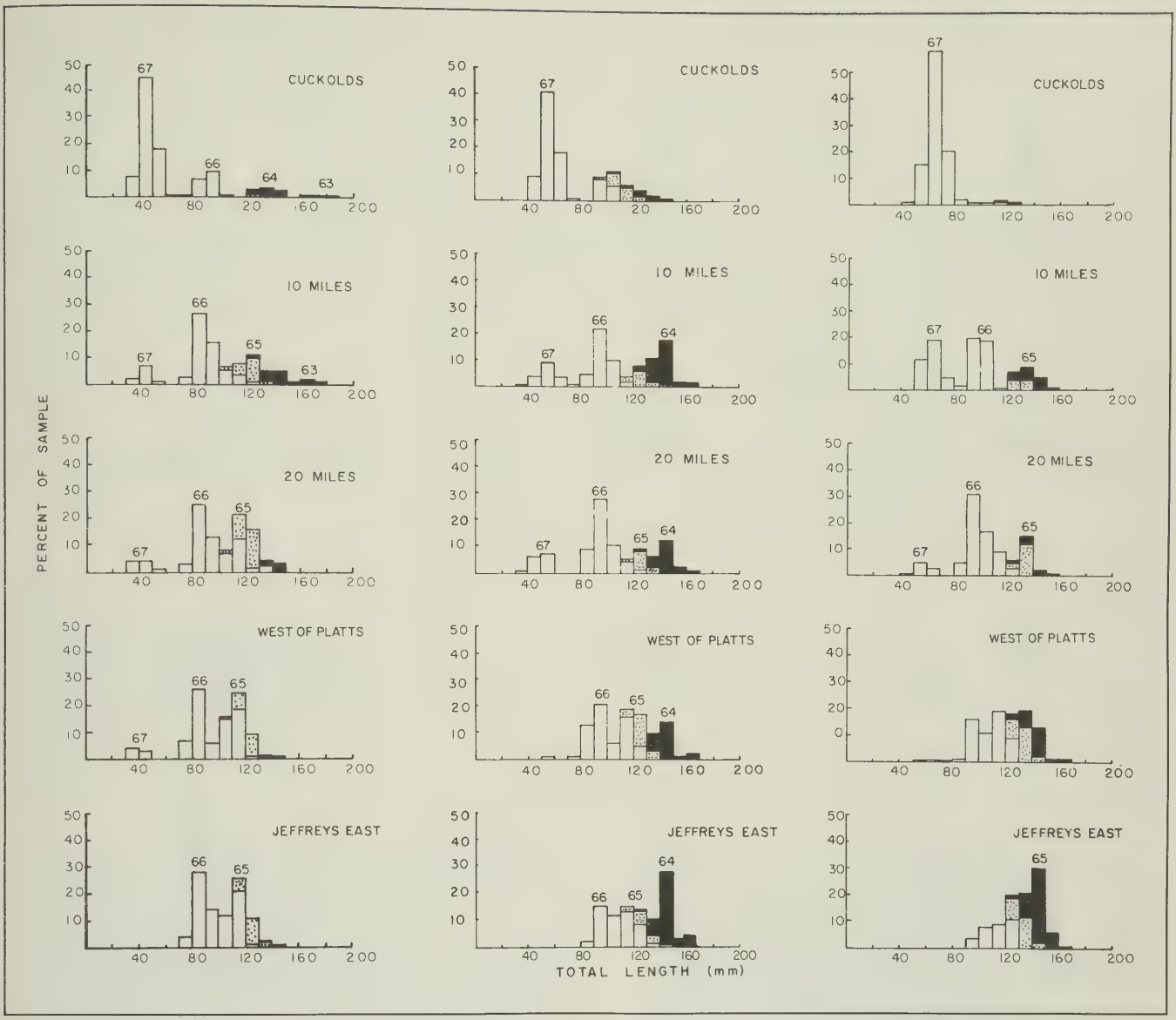


**Figure 8.—Length frequency distributions for *Pandalus borealis* sampled at inshore and offshore locations in the Gulf of Maine: from left to right, 5-6 March 1968, 14-15 May 1968, and 12 June-1 July 1968. 1963-67 year classes are labeled in cases where they were clearly identifiable. White = juveniles and males; stippled = transitionals; black = females.**

class could not be distinguished from younger and/or older year classes. A significant percentage of the 2 and 3-group shrimp belonging to this year class which were sampled during 1967-68 were in various stages of sexual transition; thus, length frequency data for this year class, particularly data collected in May at Cuckolds and at Platts and Jeffreys East in June (Fig. 8), included male, transitional, and female shrimp. The identity of the 1965 year class was further obscured by overlap with length frequency data for the 1964 year class in some samples. On the occasions when the 1965 year class was clearly distinguishable, it made up approximately 40-60% of the Platts and Jeffreys East samples and also accounted for a significant proportion of the shrimp collected at 10 and 20 miles. A small proportion of the shrimp which were collected at Cuckolds in late December and early February apparently belonged to this year class. If so, the offshore migration of younger shrimp was not completed by the third summer, since a few 2-group shrimp remained in inshore waters, and, judging by the presence of transitional individuals, changed sex during their third winter. The alternative hypothesis is that offshore migration is indeed completed by the third summer (note the almost complete absence of shrimp >80 mm TL in inshore waters in the summers of 1966 and 1967 in Figure 9), and that shrimp >100 mm TL at Cuckolds in the winter represented transitionals and females which migrated offshore as males or juveniles sometime during their first 2 years of life and then returned inshore. Such a migration is inferred for the females based on the interpretation of length frequency data for the 1964 year class, but not for transitionals.

Even though it was not possible to determine from these data at what time of year sex transition begins, it is clear that it begins in the third year of life and continues into the fourth year. It also takes place in both inshore and offshore waters. The low proportion of transitional individuals at Cuckolds, however, and their increased proportions in the offshore samples (Figs. 7, 8, 10, 11) indicated that most sex transition takes place following the offshore migration of the males. Transitional shrimp appeared in length frequency data either as 2 or 3-group shrimp during 1967-68.

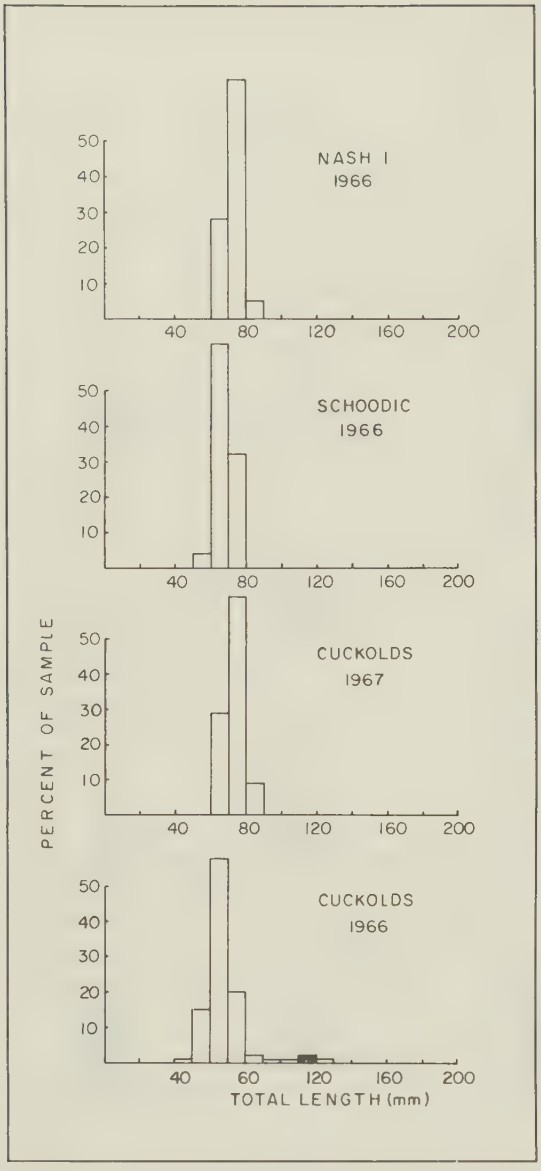


**Figure 9.—Length frequency distributions for 1-group juvenile and male *Pandalus borealis* sampled in various inshore waters during the summers of 1966 and 1967. White = juveniles and males; stippled = transitionals; black = females.**

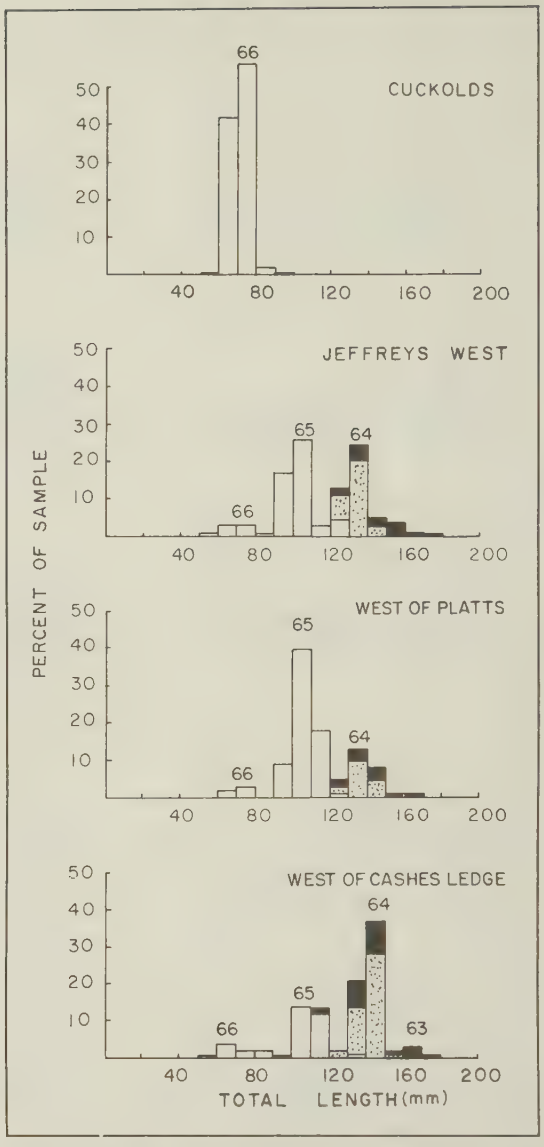


**Figure 10.—Characteristic length frequency distributions for *Pandalus borealis* collected in the summer of 1967 from four distinct inshore and offshore areas in the Gulf of Maine. Clearly identifiable year classes are labeled. White = juveniles and males; stippled = transitionals; black = females.**

The 1964 year class was represented at all sampling locations as 3-group females in the winter of 1967-68 and in May and June 1968 as 4-group females (Figs. 7, 8). The proportion of females collected at Cuckolds, 10, and 20 miles in March was very low. Females were present offshore in the summers of 1967 and 1968 (Figs. 10, 11), but were entirely absent from inshore stations in the summers of 1966 and 1967 (Figs. 9, 10). Some of the smaller females that appeared after March were presumably new 3-group (1965 year class) females which underwent sex transition during the winter and spring. Most of the females which spawned during 1967 belonged to the 1964 year class (age 3) but there were also a few older (1963 year class) females collected at Cuckolds and 10 miles in March. At least some of these older females were presumed to be repeat spawners which spawned originally in 1966.

An inshore spawning migration of females during the winter was deduced from the observed changes in the proportions of females sampled at the various sampling locations visited during 1967-68 (Figs. 7, 8, 10, 11). Female shrimp belonging to the 1964 year class accounted for 50% of the Jeffreys East sample in November. The relative abundance of this age group at this location declined dramatically to <10% in late December and early February, partially in response to the arrival of 1-group shrimp from inshore waters. Meanwhile, the percentage of 4-group females remained stable at Platts and 20 miles throughout the winter, but increased at 10 miles from November through February (at the same time that 1-group shrimp were diminishing in importance). There was no discernible change in the percentage of females at Cuckolds between late December (no sample was collected in November) and May. The low proportions of 3-group females at the inshore station was in large part due to the large numbers of 0- and 1-group shrimp in the samples. By June, however, there were almost no females at Cuckolds. No females were collected inshore in either the summer of 1966 or 1967 (Figs. 9, 10). The absence of females from Platts and Jeffreys East in March and their reappearance in

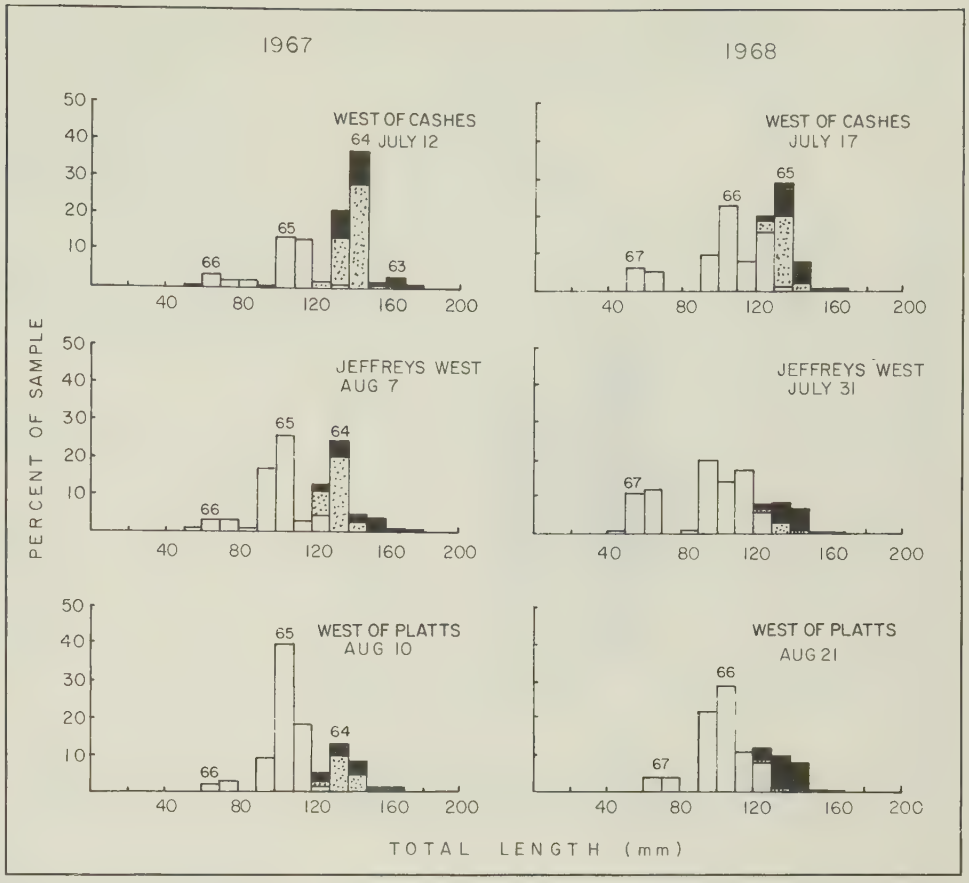


**Figure 11.—Length frequency distributions for *Pandalus borealis* collected in offshore areas of the Gulf of Maine in the summers of 1967 and 1968. Clearly identifiable year classes are labeled. White = juveniles and males; stippled = transitionals; black = females.**

May (Fig. 8) are attributed to both the return offshore migration of surviving "spent" females (1964 year class) and the sexual transition of younger (1965 year class) shrimp in the spring.

**Diurnal vertical migration**—No shrimp were taken at any depth in Jeffreys Basin in August during daylight hours, but immediately after sunset a few shrimp were caught at 180 m; by midnight, large numbers of shrimp were caught between 45 and 120 m at temperatures of 3°-4°C (Fig. 12). Shrimp were caught from 45 m to the bottom at 0400 hours. At no time were any shrimp caught in the upper pot (25 m). Except for one female, all the shrimp caught were males. Females captured in bottom trawls at the same time of year had full ovaries and were on the verge of spawning.

Females were caught in pots also fished at 9 m intervals on March 20-21 1968 in 83 m of water in the Sheepscot River. The maximum number was taken in the pot nearest the surface at midnight. Females caught in the pots had shed almost all their eggs, but a substantial number in a bottom trawl sample still retained eggs. A total of only three males were caught in pots and a trawl sample showed there were few males present on the bottom.

Male, transitional, and female shrimp were caught in pots fished at 18 m intervals in 165 m of water 20 miles south of Boothbay Harbor on 13-14 May 1968. Once again, the largest number was taken near the surface at midnight. Two similar trials in July 1968 at the same location showed that males, transitionals, and females rose toward the surface at night, but the thermocline was well developed and, as in August 1967, no shrimp were taken in the nearsurface waters where temperatures were higher than 5-6°C. It appeared that isothermal conditions permitted males and nonovigerous females to reach surface waters in March and May, but that the well developed thermocline in July and August limited the upward migration of male and female shrimp.

These observations indicated that male shrimp carry on nocturnal vertical migration throughout the year, and that female shrimp migrate through the water column when not carrying eggs. Since the egg mass on the swimming legs must be a handicap in swimming, it is not surprising that ovigerous females do not migrate far from the bottom. Lack of vertical migration by females, rather than lack of attraction to baited pots, is the likely explanation for absences of females in these vertically deployed pots, since females were feeding at the time of these trials.

**Temperature effects**—Our results showed a correlation between temperature and the horizontal and vertical migrations of *P. borealis* in the Gulf of Maine. Some shrimp migrate offshore during their first year of life; others remain inshore until sometime during their second or third years of life. During the inshore phase of the life cycle, they are subjected to a wide range of temperatures. Mean monthly bottom temperatures at Cuckolds in 1967-68, for instance, varied from 1° to 9°C, whereas bottom temperatures recorded at offshore stations ranged from 2° to 6°C (Fig. 5). Similarly, the daily vertical migrations of shrimp collected in August 1967 were limited to temperatures of not more than 5-6°C (Fig. 12). These data suggest that northern shrimp, after a certain stage in their life cycle, are less tolerant of warmer temperatures. Avoidance of warmer temperatures by older shrimp which have migrated offshore is also indicated by results which showed an inverse relation between relative catch rates and bottom temperatures between 1.5° and 6°C in June and July 1968 (Fig. 13): highest catch rates in July were obtained at 3°C. (No attempts were made to fit a linear

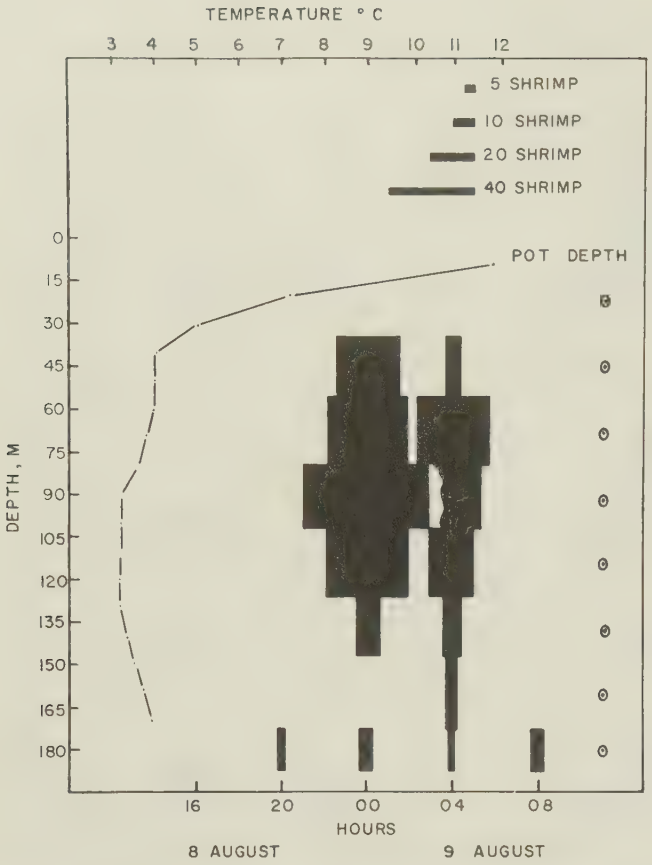


**Figure 12.—Vertical distributions of *Pandalus borealis* and temperature profile in Jeffreys Basin in August 1967. Widths of bars indicate number of shrimp caught per pot at hour indicated.**

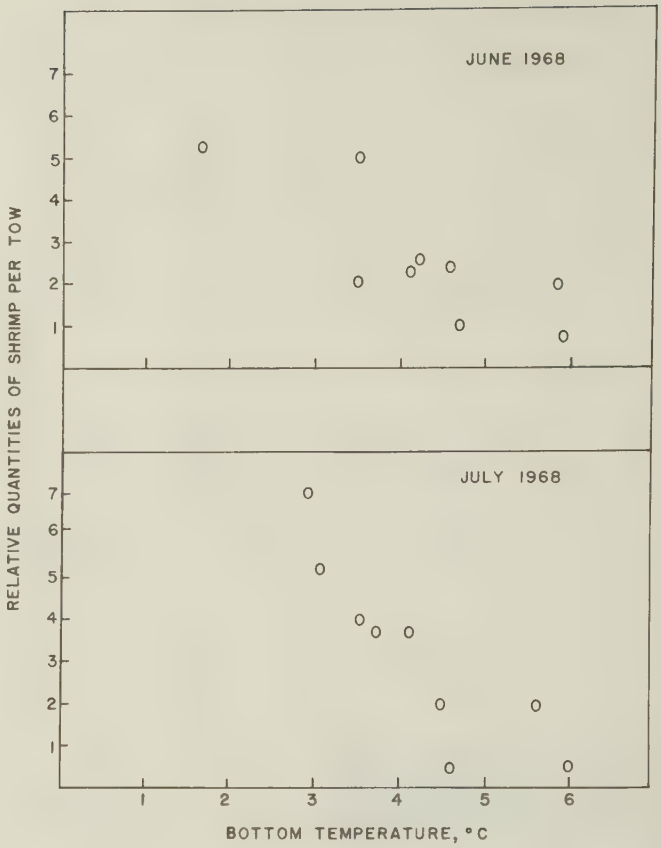


**Figure 13.—The relation between bottom temperature and the relative quantities of *Pandalus borealis* collected at all sampling locations in the Gulf of Maine, June and July 1968.**

regression to these data since there was no reason to suspect that catch rates continue to increase below 3°C.)

In their third winter, after mating, male shrimp remain offshore and undergo transition to female shrimp. In 1967-68, bottom temperatures in offshore waters in midwinter did not generally fall below 4-5°C, and remained 2-3°C warmer than in inshore waters (Fig. 5); thus, the majority of the transitional shrimp were concentrated in the warmest areas to be found at that time of year. The inshore migration of ovigerous females in the late fall and early winter may be triggered by declining bottom water temperatures in some offshore locations, such as west of Jeffreys Ledge (Fig. 5); in other offshore locations (Platts, Jeffreys East), however, bottom temperatures remain more or less constant throughout the year. Whatever the role temperature changes may play in stimulating inshore and offshore migrations of *P. borealis* in the Gulf of Maine, one of the consequences of the inshore spawning migration is that egg-bearing females and hatching larvae are exposed to colder bottom water temperatures (1°-2°C) than exist elsewhere in the Gulf during the winter and early spring.

## Geographical distribution by season

In the summer, the smallest age group (1-goup) was found almost exclusively inshore (Figs. 9, 10). These young shrimp were found offshore only in small numbers, in most cases not exceeding 10% of the offshore samples. The samples from Three Dory Ridge (Fig. 14) showed what appeared to be the typical change in age composition offshore during the summer and early fall. Similar conclusions were drawn from data collected at other offshore locations (e.g., stations 6, 8, and 9), although size distributions from different locations did not always show the same patterns at the same time. Offshore samples early in the summer tended to be dominated by 3-group transitionals and 4-group females. As the summer progressed, however, 2-group males made up a growing proportion of the samples, reflecting their continuing offshore migration that began in the previous winter, until they dominated samples taken at the end of the summer. At most offshore stations during the summer, 1-group shrimp either were not collected at all or made up a relatively small percentage of the samples (Figs. 10, 11, 14).

Three size groups dominated inshore samples collected during the winter and early spring at Cuckolds (Figs. 7, 8), as compared with inshore summer samples which contained, almost exclusively, 1-group male shrimp (Figs. 9, 10). As many as five age groups may have been present at Cuckolds in the winter of 1967-68. Most of these shrimp were males (or juveniles), but some were also transitionals and females. Two size groups of females were present in March, presumably 4 and 5-group shrimp (1 March birthday) belonging to the 1963 and 1964 year classes. As noted previously, the growing percentage of 0-group shrimp at Cuckolds during the winter was believed to be a consequence of increasing retention of smaller shrimp in the trawl as they grew larger, as well as a continuing offshore migration of 1-group males, the winter mortality (partly from fishing) of ovigerous females, and the return offshore migration of the surviving females which no longer carried eggs.

Three size groups were also present in samples from a number of offshore stations during the summer and winter, but the summer samples were dominated by the older size groups (Figs. 10, 11) and the winter samples by the two younger groups (Fig. 7). This difference in age composition is attributed to the continuous offshore migration of males and the inshore migration of females in the fall and winter. At Three Dory Ridge, on the other hand, most of the shrimp collected between January and September (Fig. 14) belonged to two size groups (rather than three). Aside from changes in the mean size due to growth, the major changes between winter and summer at this station were the increasing importance of 2-group males during the summer and fall and the absence of females in February. These changes reflect the same migratory movements of males and females noted previously.

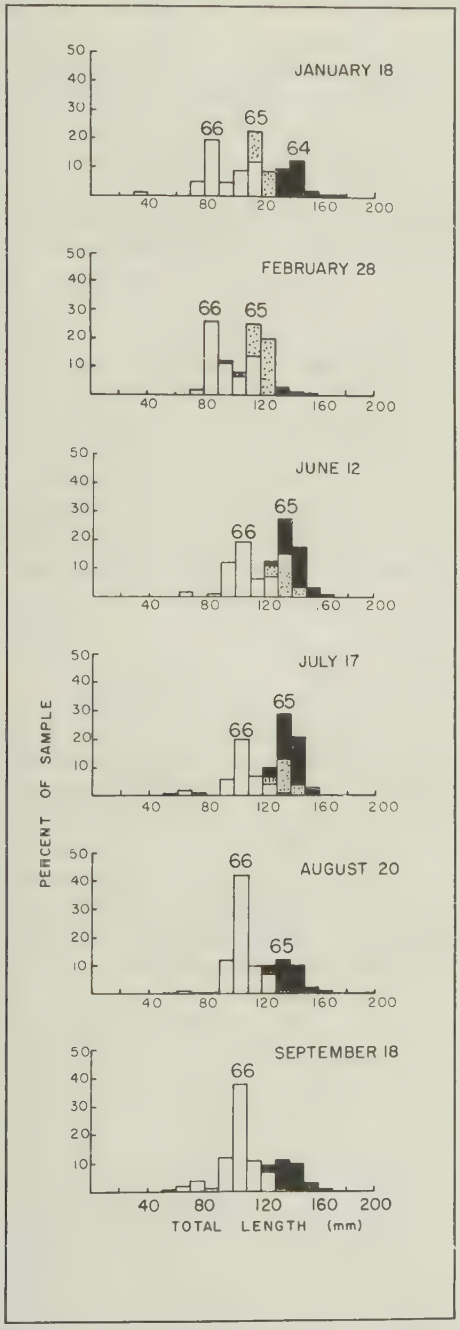


**Figure 14.—Length frequency distributions for *Pandalus borealis* sampled east of Three Dory Ridge (station 7) on various dates in 1968. Clearly identifiable year classes are labeled. White = juveniles and males; stippled = transitionals; black = females.**

## Spawning time

The timing of egg extrusion appears to be influenced by prevailing water temperatures. Eggs first appeared on the pleopods of some females collected in mid-August 1966, 1967, and 1968 at various sampling locations. The percent of ovigerous females in samples from different locations varied from <5% to 55% in August 1968 and exceeded 90% for all but two samples in September of the same year (Fig. 15). The data indicated that the time of egg extrusion was inversely related to bottom water temperature: the predicted frequency of ovigerous females in August declined from 40% at 3.6°C to 20% at 5°C. In September, over 90% of the females collected at stations with bottom temperatures <5°C were ovigerous. Of all the females collected at all stations in August 1968 and September 1967, a significantly larger percentage of those <150 mm TL were ovigerous than were females >150 mm TL (66.1% vs. 61.3% in September, and 30.1% vs. 20.6% in August). Females <150 mm TL were presumed to be a year younger than females >150 mm TL (see the March 1968 length frequency data in Figure 8)[5]. The data therefore suggest that the older (5-group) females

[5]Since these samples were processed, McCrary (1971) has described a more reliable method for distinguishing between non-ovigerous females which have or have not carried eggs previously, based upon the presence or absence of sternal spines.

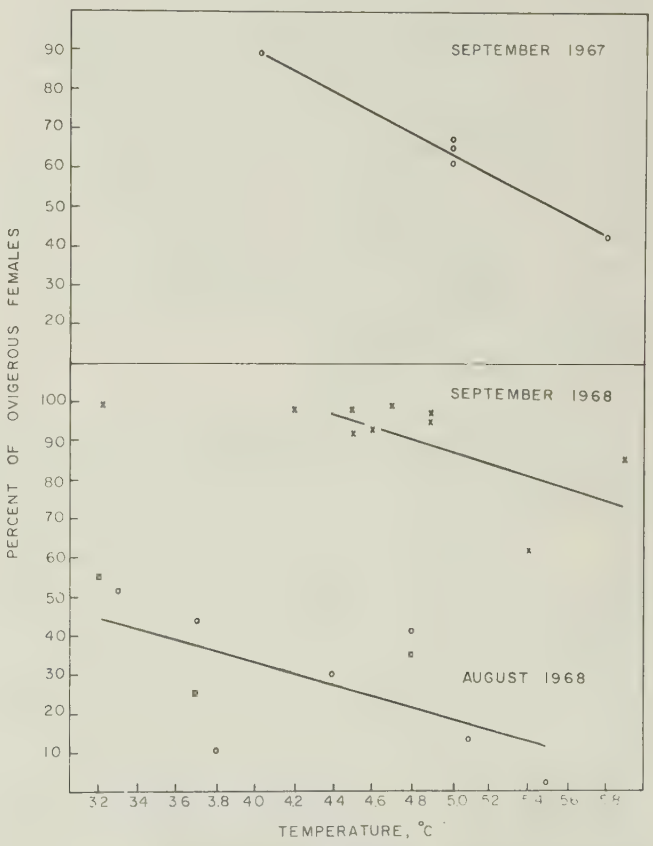


**Figure 15.—The relation between bottom temperature and the relative abundance of ovigerous female *Pandalus borealis* from various locations in the Gulf of Maine, August 1968 and September 1967 and 1968. Linear regressions for September were fit by eye; the regression for August was calculated.**

spawned later than the younger (4-group) females. The time delay in spawning between the two age groups could not be estimated.

## Age-at-maturity

Length frequency data compiled for male, transitional, and female shrimp during this study (Figs. 7, 8, 10, 11, 14) suggested that *P. borealis* in the western Gulf of Maine mature and spawn for the first time as females in their fourth year. As indicated by sample length frequency data for March and May 1968 (Fig. 8), some females apparently survive their fourth birthday to spawn a second time during their fifth year. Clearly, however, the majority of the females sampled during this study matured for the first time during their fourth year. It is not known if sex transition is delayed for some individuals until the fifth year; if so, this would also account for the presence of the older age group of females in inshore waters in the spring.

## Food and feeding

Most of the shrimp stomachs examined in this study were either empty or contained mud, or mud and unrecognizable debris. The percent of empty stomachs in all samples varied between 3% and 67% (commonly 20-40%); stomachs with only mud, or mud debris, were found in 8-55% of the shrimp examined (commonly 30-40%). Polychaete remains were found in up to 15% of the stomachs examined in any one sample, but most commonly occurred in 3% or less of the stomachs examined. Generally, less than 1% of the stomachs examined contained foraminifera as the major food item. There was a significant seasonal variation in the consumption of the two major food items (Table 3): molluscs (primarily benthic species) predominated in the winter while crustaceans (primarily pelagic species) formed most of the food in the spring and summer. There were no clear differences in the fall. Diet also depended on location. From the end of December 1967 through early March 1968, there were significant differences in the proportion of shrimp feeding on molluscs and crustaceans at Cuckolds and 20 miles: 14.2% of the stomachs contained shells at the inshore station and 4% at the offshore station, while 9.6% contained crustacean remains offshore and 5% inshore.

**Table 3.—Seasonal differences in the relative abundance (percent occurrence) of shells and crustaceans in the stomachs of *Pandalus borealis* in the Gulf of Maine, 1966-68.**

| | 1966 | | 1967 | | 1968 | |
|---|---|---|---|---|---|---|
| Season | % shells | % crustaceans | % shells | % crustaceans | % shells | % crustaceans |
| Winter | — | | 16.9 | 8.8 | 13.1 | 9.9 |
| Spring | — | — | 7.4 | 14.6 | 5.7 | 15.0 |
| Summer | 5.7 | 18.4 | 2.9 | 11.5 | 2.5 | 13.9 |
| Fall | 14.1 | 13.4 | 9.1 | 9.2 | 6.8 | 4.5 |

The difference in the relative abundance of shrimp feeding on molluscs and crustaceans at inshore and offshore stations in the winter was attributed to differences in feeding habits of female and non-female shrimp rather than differences in availability of the two food sources. Significantly more females (15.6%) collected at Cuckolds and 20 miles in the winter of 1967-68 contained mollusc shells than did non-females (5.5%). Since females and non-females were present at both stations in the winter (Fig. 7), the possible effect of prey availability at the two locations was ruled out. A more plausible explanation is that since female shrimp are bearing eggs in the winter, and since they do not migrate vertically when ovigerous, they are restricted to benthic food. Non-females migrate vertically and thus are less likely to feed on benthic molluscs. Females presumably resume feeding in the water column once the eggs hatch, thus explaining why the entire population shifts from a predominantly benthic (molluscan) diet in the winter to a pelagic (crustacean) diet in the spring and summer.

## Growth

Size-at-age estimates compiled from 1966-68 length frequency data (Fig. 16) revealed a three-fold increase in length from an age of 7 months through the end of the third year. Growth was much more rapid in the first 2 years (12 and 9 mm CL, respectively) than in the third year (3 mm CL), and was more rapid during the fall (October-November) and the spring (May-July) than during the winter or summer. Rapid growth in the fall was associated with maximum bottom water temperatures at inshore and offshore locations (Fig. 5).

Differences of approximately 1-2 mm CL (5-10 mm TL) were evident in length frequency data for the same age groups sampled at different locations in the spring and summer of 1968 (Figs. 17, 18) and in March 1967 and 1968 west of Jeffreys Ledge (Fig. 19). Comparison of water temperatures recorded at different depths at Three Dory Ridge and west of Jeffreys Ledge 4 months prior to collection (Fig. 18) and west of Jeffreys in May of 1967 and 1968 (Fig. 20) revealed that increased size-at-age is correlated with higher temperatures and suggested that growth is positively related to temperature.

## Sex transition

Length frequency data collected from Jeffreys West in March 1967 not only provided evidence for more rapid growth compared with March 1968 data, but also showed an increased proportion of transitional and female shrimp (Fig. 19). Bottom temperatures were 1°C warmer in May 1967 than in March, April, or May 1968 (Figs. 18, 20). These results suggested that either the rate of sex transition was reduced or sex transition was delayed at lower temperatures, and that the increased percentage of transitional and female shrimp was associated with increased growth rates at higher temperatures.

The same conclusion was reached after comparing the proportion of transitional shrimp on the east and west sides of Jeffreys Ledge in the spring of 1968. In April of that year the bottom water on the east side of the Ledge was about 3°C warmer and the whole water column between 50 and 140 m was approximately 1°C warmer than on the west side (Fig. 20). The percentage frequency of transitional shrimp east of the Ledge was significantly greater on two occasions during March and April 1968 (29.9% vs. 19.7% in March, and 19.3% vs. 10.7% in April). Similar differences in the proportion of transitional and female shrimp west of Jeffreys Ledge and east of Three Dory Ridge in July 1968 were positively associated with a 1°C difference in spring water temperatures between 80 and 180 m (Fig. 18). In contrast, the difference in the proportion of transitionals sampled during March 1968 between Platts Bank (26.3%) and east of Jeffreys Ledge (29.9%), two locations where temperature differences were small, was not significant.

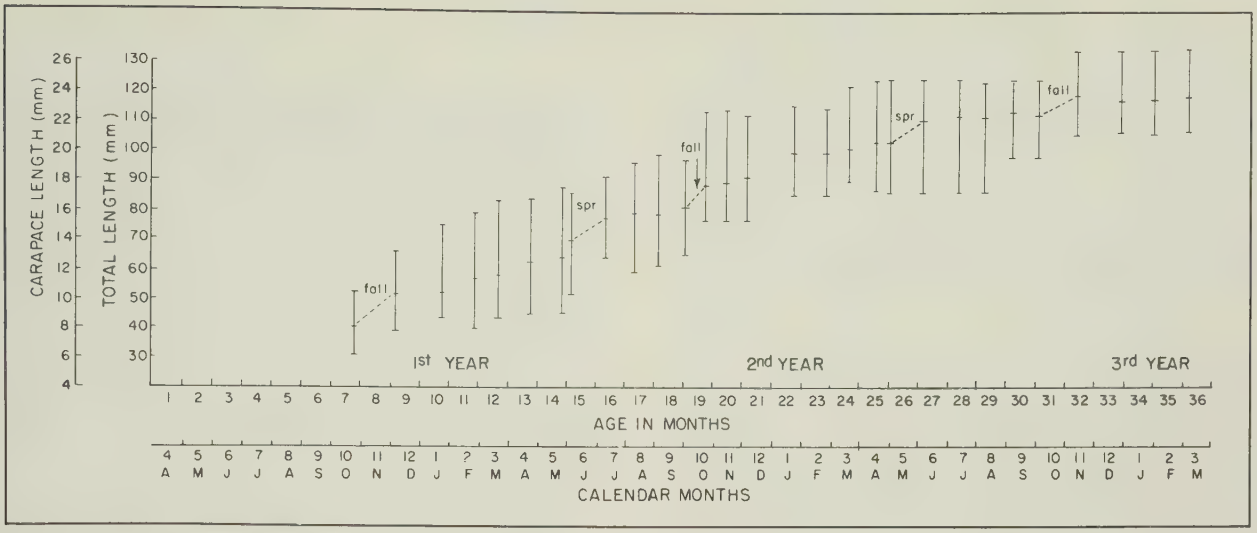


**Figure 16.—*Pandalus borealis* mean length-at-age and growth history for the first three years of life estimated from length frequency data collected at various locations in the Gulf of Maine during 1966-68. Periods of more rapid growth are indicated by dashed lines.**

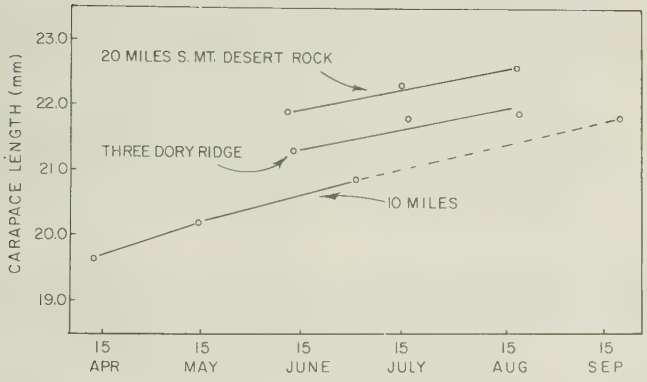


**Figure 17.—The growth of 2-group *Pandalus borealis* at three locations in the Gulf of Maine in the spring and summer of 1968.**

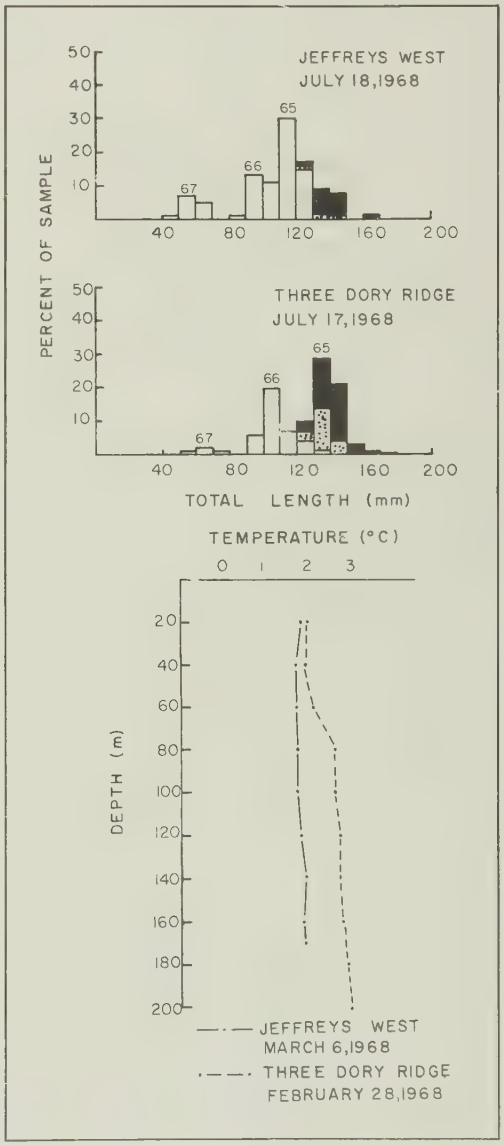


**Figure 18.—*Pandalus borealis* length frequency distributions and year classes from west of Jeffreys Ledge and east of Three Dory Ridge in July of 1968 with vertical temperature profiles from the same two locations in February and March of the same year.**

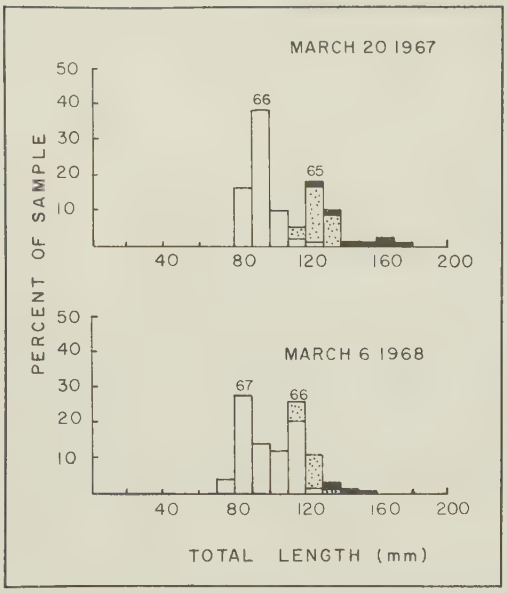


**Figure 19.—Length frequency distributions and year classes of *Pandalus borealis* collected west of Jeffreys Ledge in March 1967 and 1968.**

## Fecundity

Linear regressions were fitted to nine sets of fecundity data compiled for eight different locations in August and September 1968, but covariance analysis revealed that among locations within each month neither intercepts nor slopes were significantly different. The predicted mean fecundities of intermediate-sized (30.25 mm CL or 150 mm TL) shrimp were greater ($P < 0.10$) in August west and east of Jeffreys Ledge than at 20 miles or Fippennies (Table 4). In September, 150 mm TL shrimp collected from Three Dory Ridge were more fecund ($P < 0.10$) than shrimp of the same size from Cashes Ledge, but not from west of Jeffreys and two other locations. There were no differences in fecundity between samples for smaller or larger shrimp in either month, even at the 90% confidence level. These weak differences in fecundity between locations could not be correlated with differences in bottom water temperatures during the period of egg development (May-August). The apparent difference in predicted mean egg numbers for 150 mm TL shrimp collected west of Jeffreys Ledge between August (1875) and September (1740) was not significant even at $P = 0.10$, nor was the difference between August 1966 (1980) and August 1968 (1875).

Results of fecundity estimates for all ovigerous shrimp ($N = 202$) collected in 1968 were quite variable: there was as much as a twofold difference in observed egg numbers among individual shrimp of a given length. Despite this variability, statistically significant ($P < 0.05$) linear and log linear regressions were fitted to the combined data set. Predicted mean egg numbers (linear model) ranged from 1,000 for 25 mm CL (124 mm TL) females to 2,400 for 35 mm CL (173 mm TL) females (Fig. 21).

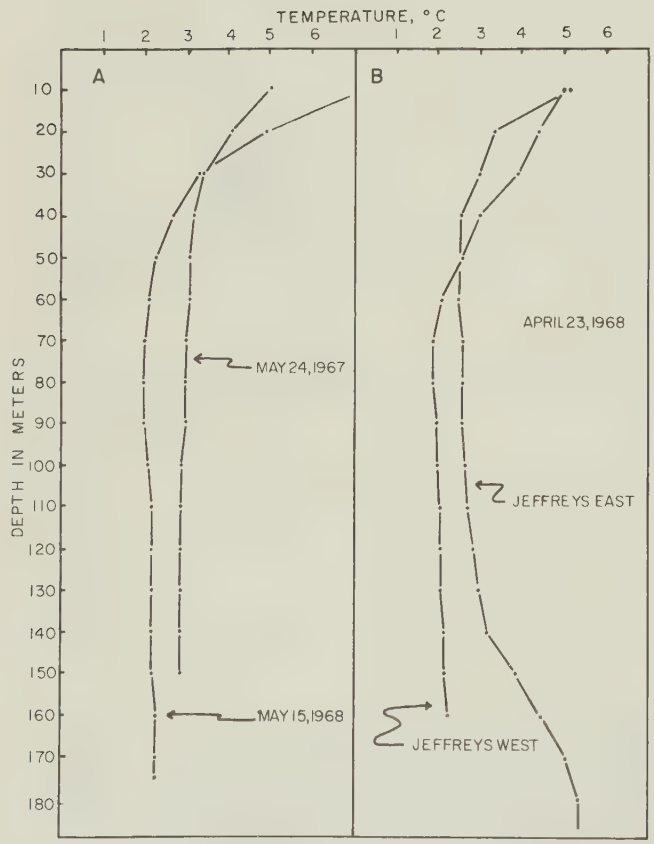


**Figure 20.—Vertical temperature profiles west of Jeffreys Ledge in May 1967 and May 1968 (A) and on each side of Jeffreys Ledge in April 1968 (B).**

**Table 4.—Predicted mean number of eggs per 150 mm TL (30.25 mm CL) female *Pandalus borealis* collected in eight different locations in the Gulf of Maine, August and September 1968.**

| Location (Station) | *n* | Predicted mean number of eggs/150 mm female |
|---|---|---|
| **August** | | |
| 20 miles south (3) | 19 | 1,535 |
| Fippennies (8) | 9 | 1,575 |
| East Jeffreys (6) | 18 | 1,825 |
| West Jeffreys (5) | 17 | 1,875 |
| **September** | | |
| Cashes Ledge (10) | 39 | 1,680 |
| West Jeffreys (5) | 50 | 1,740 |
| West of Platts (4) | 23 | 1,815 |
| 10 miles south (2) | 12 | 1,880 |
| 3 Dory Ridge (7) | 15 | 1,925 |

**Figure 21.—Fecundity data for 202 *Pandalus borealis* collected in eight different locations in the Gulf of Maine, August and September 1968 (see Table 7) with least squares linear regression model $Y = -2633.9 + 145.1\ X$, where $X$ equals lateral carapace length.**

## Egg parasitism

Once eggs are spawned, they are susceptible to infestation by a number of epizoic organisms (e.g., filamentous bacteria, suctorians, and peritrich protozoa) which attach externally to the egg mass and by an internal peridinian dinoflagellate parasite (Stickney 1978). This internal parasite causes egg mortalities which are indicated by the appearance of large, white (or opaque) eggs.

Two ovigerous females were collected 7 August 1967 in Jeffreys Basin. By the first half of September, many females collected in offshore waters were ovigerous. Egg development, then in stage 1, appeared normal on all females examined. By early October, when 99% of all females were ovigerous and when eggs were in early Stage 2, large, opaque eggs appeared in the egg masses and the proportion of sampled females carrying infected eggs was progressively higher further west along the coast, increasing from 23% of all females examined south of Matinicus Island to 63% in Jeffreys Basin (see Figure 4). Although temperature measurements were not made at these locations in October 1967, this trend was inversely related to the usual trend in fall bottom water temperatures which generally decline by 1°-2°C from east to west along the Maine coast (Colton and Stoddard 1973)[6]. In late October, all egg development had reached Stage 2 and, while the proportion of females with at least a few white eggs west of Platts Bank remained between 40% and 50%, the proportion of females at the 20 mile station carrying internally parasitized eggs increased from 30% early in October to 83% at the end of the month.

In mid-November, as females moved to within 10 miles of the coast (station 2), about 6% of the eggs sampled at that location had reached the eye pigment stage and 73% of the ovigerous females carried some white eggs. In early December, all eggs had reached the eye pigment stage and 70% of the females carried at least a few white eggs. At this time, an unidentified stalked and vorticellid protozoan appeared in 6% of the egg masses which already included internally parasitized eggs. On 19 December, a sample from inshore waters contained 87% females with some white eggs, and 15% of the egg masses containing white eggs were also infested with the stalked protozoan. Off Platts Bank on 21 December 1967, 30-40% of the females sampled carried some white eggs, but no vorticellids were found. On 27 December, close inshore, 46% of the females carried eggs infested with vorticellids.

By late December it was obvious that many females were carrying fewer than the expected number of eggs. Egg loss was attributed in part to the continuous proliferation of internal parasites and perhaps also to the increased incidence of the external (vorticellid) protozoans, although the effect of the vorticellids on egg viability is unknown. Vorticellid infestation and internal parasitism appeared to peak in January; a sample from inshore waters on 19 January 1968 showed 49% females with internally parasitized eggs, and 61% of these were infested with protozoans. At the same time, egg losses appeared to be reduced.

White eggs and vorticellid infestations were still observed during February and March 1968, but at reduced incidence; a sample taken inshore on 5 February showed 12% females with white eggs, and 10% of these were also infested with external protozoans. At this time, most of the non-parasitized eggs had reached early stage 4 with about a month of development remaining. A few females had shed almost all their eggs, and these invariably had many protozoans attached to the pleopods. On 29 February, 2% carried white eggs and 4% of these carried protozoans. In mid- and late March, both afflictions were extremely rare.

It is clear that ovigerous shrimp migrating inshore from October through December in 1967 and 1968 moved from colder to warmer waters (see Figure 5). Average offshore fall bottom temperatures were about 4°-5°C, while inshore fall bottom temperatures reached 7°C at Cuckolds and probably higher further inshore. The development of egg parasites may be associated with this rise in temperature encountered during inshore migration. There was an apparent relationship in late December 1967 and in November and December 1968 between bottom water temperatures and the percentage of females with externally parasitized eggs collected in various locations (Table 5). It appeared that there was little or no infestation at temperatures of 5.5°C or less, and considerable infestation (3-48%) at temperatures above 5.5°C. The highest incidence of infestation occurred at temperatures of 7°-9°C. A clear relation between external egg infestation and temperature was not evident after December 1967 when inshore bottom temperatures dropped rapidly, but it is very likely that infested eggs which were still being carried by female shrimp after December had been infested earlier when temperatures were higher. The progressive reduction in infestation and the nearly total absence of parasitized eggs in February and March, when low temperatures prevailed, support this hypothesis.

The same sequence of events, i.e., the development of internal egg parasites in ovigerous shrimp migrating into inshore waters followed by infestations of the egg mass by epizoic vorticellids and egg loss was again observed in the following year (October to December 1968). The effect was apparently even more intense than in 1967, possibly as a result of the warmer inshore water temperatures which prevailed in 1968 (see Figure 5).

[6]The fact that colder temperatures are associated with slower rates of parasite development explains why the percentage frequency of infected eggs would be higher at any point in time on females in colder water (Stickney 1981). Egg mortality may be more severe in warmer water due to increased parasite development rates.

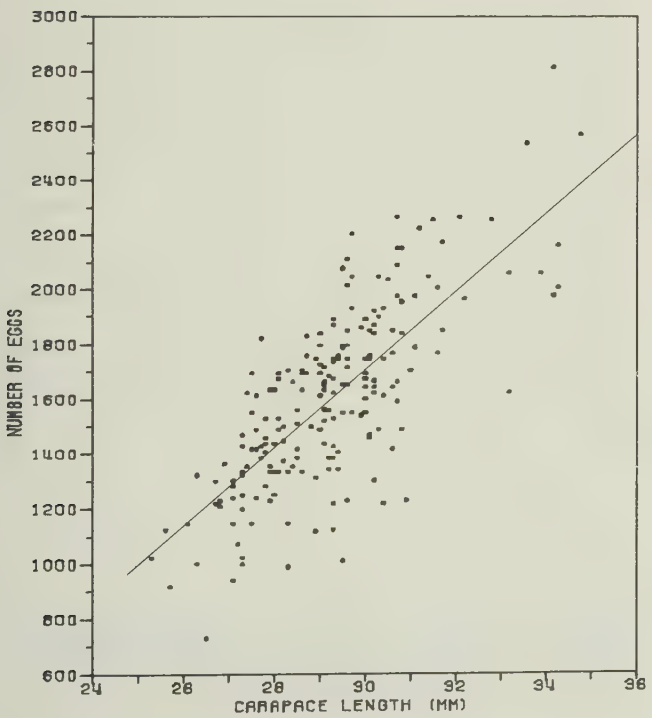

Table 5.—Bottom temperatures and percent of female *Pandalus borealis* with epizoic protozoans on their eggs at various locations in the Gulf of Maine, 1967-68.

| Station no. | Date | Temp. (°C) | % females with infested eggs |
|---|---|---|---|
| 5 | 7 Nov. 1968 | 4.3 | 0 |
| 6 | 6 Nov. 1968 | 4.4 | 0 |
| 4 | 6 Nov. 1968 | 4.9 | 0 |
| 3 | 27 Dec. 1967 | 4.9 | 1 |
| 4 | 3 Dec. 1968 | 5.0 | 1 |
| 6 | 3 Dec. 1968 | 5.1 | 0 |
| 4 | 21 Dec. 1967 | 5.2 | 0 |
| 6 | 21 Dec. 1967 | 5.3 | 0 |
| 7 | 18 Jan. 1968 | 5.5 | 0 |
| 5 | 21 Dec. 1967 | 5.6 | 6 |
| 3 | 27 Dec. 1967 | 5.9 | 5 |
| 3 | 19 Dec. 1968 | 6.8 | 4 |
| 1 | 27 Dec. 1967 | 7.1 | 46 |
| 1 | 19 Dec. 1968 | 7.2 | 48 |
| 2 | 19 Dec. 1968 | 7.4 | 8 |
| 2 | 21 Nov. 1968 | 8.1 | 3 |
| 1 | 21 Nov. 1968 | 8.6 | 40 |

## DISCUSSION

The results of this work have revealed several important life history characteristics of the northern shrimp population in the Gulf of Maine which are affected by temperature and provide some basis for predicting how low temperatures might possibly stimulate population growth. Attention has focused on several factors which affect the reproductive potential of this population, i.e., migratory behavior, egg parasitism and mortality, spawning times, growth rates, and the timing and/or rate of sex transition.

In further examining the effects of temperature on various life history characteristics of *Pandalus borealis*, a great deal may be inferred from studies carried out in other locations. Two of the most fundamental characteristics which have been shown by a number of authors to vary over the geographic range of the species are growth and longevity. In general, growth in more northern latitudes is slower than in more southern latitudes. Total length-at-age-2 estimates reported by Rasmussen (1953), for example, for the islands of Jan Mayen and Spitsbergen, were 30-35 mm lower than in the North Sea (Allen 1959) and southern Norway (Rasmussen 1953), and 50 mm lower than in British Columbia (Butler 1971) and the Gulf of Maine (Haynes and Wigley 1969 and this study). Maximum age also varies with geographic range from 3 years in the North Sea (Allen 1959) to 7½ years or older in Spitsbergen (Rasmussen 1953). The estimated maximum age for *P. borealis* in the Gulf of Maine is 5 years (Haynes and Wigley 1969 and this study).

A comparison of estimated ages at first spawning made by various authors (Butler 1964; Allen 1959; Rasmussen 1953; Poulsen 1946; Squires 1965; Horsted and Smidt 1956) for *P. borealis* populations exposed to different average annual bottom water temperatures at different geographical locations (Fig. 22) revealed that slower growing, longer lived shrimp in arctic waters mature as females at older ages than those in more temperate waters. According to the functional (logarithmic) relationship used to describe the relationship between age at first spawning and temperature (Fig. 22), a reduction of only 2°C (from 4.5 to 2.5°C) could delay maturity from age 3 to age 4 and thereby increase generation length by 1 year.

The range of annual mean fall bottom water temperatures reported by Davis (1978) for the Gulf of Maine for the period 1963-75 was 3°C (5.7°-8.6°C): a maximum change of 1°C was reported between consecutive years during this same period. The annual range of mean spring bottom temperatures during the period 1968-75 was about 1.5°C with a maximum change of 0.8°C. Evidence presented in this report does suggest that growth rates and the rate or onset of sex transition of northern shrimp in the Gulf of Maine do vary according to temperature, but it is not known whether the temperature changes reported by Davis are sufficient to also affect the age at which females mature.

An inverse relation between temperature and time of spawning has been reported by Allen (1959) and Haynes and Wigley (1969). In the cold waters of Spitsbergen and Greenland (average annual bottom temperatures of 1°-3°C), spawning occurs in July and August, but in the North Sea (average 8°-9°C), it occurs in October. Butler (1964) noted that females in the warm waters of British Columbia (average >9°C) begin to spawn in mid-November. The inverse relation between the time of spawning and temperature in different geographical areas throughout the range of *P. borealis* and in different areas within the Gulf of Maine in the same season both support the hypothesis that colder temperatures favor earlier spawning. Nunes (1984), on the other hand, reported that *P. borealis* held in the laboratory at ambient Gulf of Alaska temperatures (annual mean of 6.3°C) spawned almost 2 months earlier than *P. borealis* held at 2°-3°C and 8°-9°C.

Inshore-offshore migrations and the separation of the life cycle into inshore and offshore components have been reported in British Columbia (Berkeley 1930), Norway (Wollebaek 1908; Hjort and Ruud 1938), Korea (Kim 1966), and West Greenland (Horsted and Smidt 1956). These authors inferred an inshore spawning migration of females into shallower water and an offshore migration of males from size frequency data collected at different times of year. Some of these reported movements have been associated with temperature differences. In one case, the migration of adult shrimp into fjords on the west coast of Greenland was confirmed directly by tagging studies (Horsted 1969).

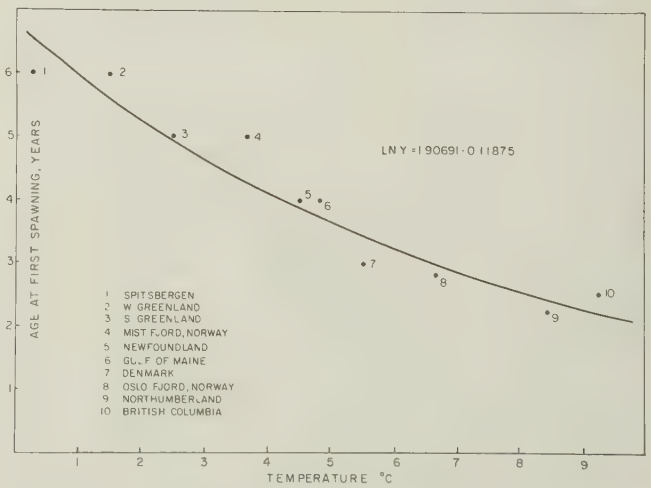


**Figure 22.—The relation between average annual bottom temperature and the approximate age of first maturity of female *Pandalus borealis* throughout the geographical range of the species.**

Barr (1970) reviewed published evidence that northern shrimp leave the bottom and rise into the upper water layers at night. Both Wollebaek (1903) and Hjort and Ruud (1938) reported the belief among Norwegian fishermen that shrimp rise off the bottom at night. Horsted and Smidt (1956) noted that Greenland fishermen have observed the same phenomenon and reported taking a few shrimp well off the bottom at night; they concluded that shrimp probably migrate in response to the upward movement of prey organisms. On the basis of catches in vertically-deployed shrimp pots, Barr and McBride (1967) and Barr (1970) have shown that in Alaska, *P. borealis* and other pandalids migrate vertically about 100 m at night. Diurnal vertical migrations have also been inferred from trawl catches. Haynes and Wigley (1969) found *P. borealis* in midwater trawls at night, but not during the day, while a number of authors have reported reduced bottom trawl catches at night (Wollebaek 1903; Hjort and Ruud 1938; Horsted and Smidt 1956; Blacker 1957; Bryzagin 1967). In another study, the relative abundance of egg-bearing females in bottom trawl catches was reported to be much lower during daylight hours when smaller non-ovigerous shrimp presumably descend to the bottom (Jones and Parsons 1978). These results and the results of this study suggest that the presence of eggs impedes swimming ability. As was observed for *P. borealis* in this study, the vertical migration of *P. jordani* off the Oregon coast was limited by a strong thermocline (Milburn and Robinson 1968). In contrast, Barr (1970) reported that the diurnal vertical migration of *P. borealis* in Alaska was unaffected by temperature variations, either seasonally or vertically.

Observations on the food and feeding behavior of *P. borealis* reported in this study were generally confirmed by Wienberg (1981) who confirmed earlier reports that in the North Sea this species is omnivorous and feeds on planktonic and benthic prey organisms. Principal prey were polychaetes, molluscs, and benthic as well as planktonic crustaceans, although diet composition was a function of prey availability, time of day, and developmental stage of the shrimp. During the night, shrimp which migrated vertically fed mainly on plankton; during the day when shrimp remained on the bottom, benthic species were ingested. Ovigerous females did not feed as actively as males.

The results of this study differed from results presented for the Gulf of Maine by Haynes and Wigley (1969) in two respects. First, length-at-age data compiled during this study showed rather slower growth for younger shrimp than did data collected by Haynes and Wigley. This difference might have resulted from the warmer temperatures of inshore waters in 1963-65 (Fig. 3) when lengths-at-age for 0 and 1-group shrimp collected by Haynes and Wigley were determined. Secondly, our results did not show a leveling-off of egg numbers for shrimp larger than 160 mm TL (32 mm CL) as was reported by Haynes and Wigley (1969)[7]. (Fecundities estimated by Haynes and Wigley did, however, include a greater percentage of larger shrimp than in this study.) More importantly, fecundities estimated by Haynes and Wigley were considerably higher at all sizes: a 160 mm TL female carried an estimated 3,000 eggs in 1963-65, and only 2,000 eggs in 1968.

[7]Figure 8 in Haynes and Wigley was corrected to account for an apparent error in the conversion from dorsal carapace length to total length.

## Correlation between temperature, population size, and landings

Examination of historical Maine landings data (Figs. 1, 2) reveals a period of increased landings in the 1940s with an absence of landings in the mid-1950s followed by a much more substantial increase in landings in the late 1960s. Although no fishing effort data were collected until 1964, fishermen reported that they continued to look for shrimp without success during 1954-57 when no landings were recorded. This information plus the observed changes in catch-per-unit-effort (CPUE) in the late 1960s and early 1970s (Fig. 3) suggested that the periods of high and low landings corresponded to periods of high and low population size. Further evidence for a reduction in population size since the late 1960s and early '70s was provided by biomass estimates for the period 1969-79 and annual trawl survey catch rates compiled since 1968 (Clark et al. 1979; Diodati et al. 1984).

Since inshore waters in winter are well mixed and generally isothermal, the monthly sea surface temperatures recorded at Boothbay Harbor are a fair indication of the temperatures to which the egg-bearing females are exposed following their inshore spawning migration in the fall. From 1906 to 1949, average monthly sea surface temperatures during January, February, and March of each year were less than 4°C (Welch and Churchill 1985). After 1954 (with one exception), the average sea surface temperatures for those months were less than 5°C and, generally (through 1980), less than 4°C. During 1950-53, on the other hand, the average sea surface temperature at Boothbay Harbor during at least one of the same 3 months was above 5°C (Table 6). Four years later (1954-57), when shrimp hatched in 1950-53 would have recruited to the commercially exploited population, no shrimp landings were recorded in Maine. The implication is that record-high inshore winter water temperatures in 1950-53 were associated with a reduction in the adult population 4 years later.

There was no clear indication of a relationship between temperature and the dramatic increase and decrease in landings and CPUE in the late 1960s and early 1970s (Fig. 3). The lack of such a relationship may have been due, at least in part, to the compounding effect of a tremendous increase in fishing effort after 1967. Anthony and Clark (1980) examined the relationship between population size, temperature, and fishing effort by comparing stock size estimates obtained from trawl surveys during this period with lagged annual effort and Boothbay Harbor sea surface temperatures (under the assumption that temperature and exploitation primarily affect recruitment 4 years later). They showed that a general decline in stock abundance between 1969 and 1975 was associated with

**Table 6.—Average monthly winter surface-water temperature (°C) at Boothbay Harbor, Maine, and shrimp landings (metric tons) 4 years later. (Temperatures >5°C are underlined).**

| Year | January | February | March | Shrimp landings 4 years later |
|---|---|---|---|---|
| 1949 | 3.6 | 2.2 | 2.8 | 17.6 |
| 1950 | 5.7 | 3.4 | 3.3 | 0 |
| 1951 | 6.1 | 4.1 | 4.7 | 0 |
| 1952 | 5.2 | 4.2 | 4.2 | 0 |
| 1953 | 4.7 | 5.5 | 6.1 | 0 |
| 1954 | 4.2 | 3.5 | 5.0 | 2.3 |

Source: Welch and Churchill (1985).

declining temperatures during 1964-67, increasing temperatures during 1967-69, and relatively stable temperatures in 1969-71. Fishing effort increased from 500 to 8,000 standard fishing days between 1964 and 1970. The general trend in annual sea surface temperatures during 1967-75 was upwards from 7.3°-9.4°C (Fig. 3) and was associated with consistently low estimates of stock abundance during 1971-79. Fishing effort declined dramatically after 1972 and remained below 500 standard days during 1977-80[8].

## Offshore habitat preferences

A number of surveys (Bigelow and Schroeder 1939; Walford 1948; Wigley 1960; Haynes and Wigley 1969) concur in showing that *P. borealis* occurs in heaviest densities in the summer in the deeper waters of the western Gulf of Maine, particularly in the vicinity of Jeffreys Ledge. Bottom trawl surveys conducted by the U.S. Bureau of Commercial Fisheries in 1967 and 1968 consistently produced large quantities of shrimp in Jeffreys Basin (U.S. Dep. Interior 1967, 1968). Catches made during the course of this study confirmed these observations: the largest catches were consistently made in Jeffreys Basin. In this study, catch rates during June and July 1968 were inversely proportional to bottom water temperatures and reached a maximum at 3°C (Fig. 13). A high concentration of shrimp in the Jeffreys Ledge area, particularly west of the Ledge and in Scantum Basin, was also indicated by bottom trawl surveys conducted by the Maine Department of Marine Resources during the period of low shrimp abundance in 1975-78 (Schick et al. 1980). The fact that this distribution pattern persisted even when population size was low suggests that it is characteristic of the population and persists regardless of changes in population abundance.

The southwestern region of the Gulf provides suitable temperature conditions to support the offshore life stages of *P. borealis*. Bottom temperatures are colder in the western sector of the Gulf, due largely to the persistence of vertical stratification during the warmer months which limits solar heating to the water mass lying above the thermocline. Further eastward along the coast, increased tidal turbulence produces greater vertical instability and more thorough mixing of surface and bottom waters throughout the year. Bottom temperatures in the eastern Gulf are therefore slightly warmer throughout the year than in the western Gulf. In addition, submarine basins which retain cold bottom waters are much more widespread in the western sector of the Gulf. Jeffreys Basin is one such area; bottom temperatures there were considerably colder during the course of this study than at other offshore sampling locations. Jeffreys Basin and other similar areas in the western Gulf can therefore be characterized as "refuges" for this boreal species, where conditions for sex transition, reproduction, and perhaps feeding are superior to other locations in the Gulf. The correlation of shrimp abundance and the high organic content of sediments reported by Bigelow and Schroeder (1939), Wigley (1960), and Haynes and Wigley (1969) may be coincidental rather than causal since partially enclosed submarine basins probably trap both sediments and cold, dense water.

[8]Estimates of total fishing effort for the period 1960-74 are from Anthony and Clark 1980; estimates after 1974 were derived from total landings and CPUE data in Diodati et al. 1984.

## Reproductive strategy

Several biological characteristics of the northern shrimp population in the Gulf of Maine may be interpreted as mechanisms selected for maximum egg production. Most importantly, pandalid shrimp are protandric hermaphrodites; each individual has reproductive potential which enables the population to exploit favorable environmental circumstances to the maximum limit. In a theoretical treatment of the selective advantages of hermaphroditism, Smith (1967) noted that synchronous hermaphroditism appears to be more advantageous for short-lived animals. With a somewhat longer life span, protandric hermaphroditism conveys reproductive advantage over synchronous hermaphroditism and bisexuality. Thus, northern shrimp, living from 3 to over 8 years in various locations in the Atlantic, have evolved the form of sexual reproduction that results in the maximum rate of population growth under favorable conditions.

Warner (1975) developed a model which accounted for age-specific differences in survival and fecundity and examined the adaptive significance of sequential hermaphroditism in terms of increased reproductive potential of individuals in the population. He concluded that the degree of selection pressure depends primarily on the fecundity schedule of the females: when fecundity increases with age and individuals mate at random (presumably true for *P. borealis*), protandry may confer a selective advantage. Furthermore, when female fecundity increases rapidly with age and/or when more age classes are represented in the population, the age of sex transition is delayed. Warner used survival and fecundity data from Haynes and Wigley (1969) to correctly predict the age of sexual transition for the Gulf of Maine *P. borealis* population[9].

A second feature of the reproductive strategy of northern shrimp in the Gulf of Maine is their migratory behavior. We have demonstrated that the distributions and migratory behavior of northern shrimp in the Gulf of Maine change with age, i.e., 0-group shrimp, for the most part, remain inshore, 1-group shrimp migrate offshore, 2-group shrimp undergo sex transition in offshore waters, egg-bearing 3-group females migrate inshore in the fall and winter where larvae hatch in the early spring, after which some return offshore to make a second (and possibly a third) inshore spawning migration. Inshore-offshore migrations and the separation of the life cycle into inshore and offshore components have been reported in British Columbia (Berkeley 1930), Norway (Wollebaek 1908; Hjort and Ruud 1938), and West Greenland (Horsted and Smidt 1956).

We conclude that the migratory behavior of *P. borealis* in the Gulf of Maine is related to seasonal and inshore-offshore temperature differences. We have suggested that the offshore migration of maturing male shrimp from inshore waters may be stimulated by a reduced tolerance for warmer temperatures as shrimp approach maturity in their second summer. Being a boreal species, *P. borealis* in the Gulf of Maine can be expected to avoid bottom water temperatures which exceed those encountered in more northern latitudes, i.e., temperatures >5-6°C. Furthermore, accelerated growth in warmer offshore waters apparently stimulates earlier (or quicker) sex transition. Stevenson and Pierce (1985) have shown that faster-growing *Pandalus montagui* change sex a year sooner than slower growing individuals in the same age group. Finally, completion of egg development during the winter in the coldest prevailing temper-

[9]It must be realized that both Smith's and Warner's approaches to modeling hermaphroditism deal with genetic reactions to long-term natural selection pressures. Changes in the timing of sexual transition may be under the influence of much more immediate short-term exogenous factors (e.g., temperature) so that differences are related to geographic distribution.

atures in the Gulf may reduce the incidence of egg parasitism and ensures that the larvae will hatch in more productive inshore waters during the period of spring plankton blooms.

## Effects of temperature on egg production

A possible effect of temperature stratification on egg production is explained in a hypothesis proposed by McLaren (1963, 1974) who argued that an energy bonus accrues to an animal which migrates upward into warmer water to feed—usually at night—and then returns to deeper, colder water during the day to assimilate its food. The mechanism proposed by McLaren to explain the results of a growth model which predicted higher rates of population increase for copepods (*Pseudocalanus minutus*) and chaetognaths (*Sagitta elegans*) which are exposed to larger temperature differentials (warmer surface water and cooler subsurface water) during vertical migration is that food is ingested more efficiently in warmer water and assimilated more efficiently in colder water. The proposed energy bonus acquired through migration and feeding in a thermally stratified water column would increase reproductive potential by reducing generation length and increasing fecundity. According to McLaren's hypothesis, diurnally migrating animals would therefore have lower fecundities if the minimum temperature occurs at intermediate depths and high fecundities if thermal stratification is stable (with the minimum temperature at the bottom). Thus, as noted by McLaren (1974), small-scale vertical temperature changes and the depth of minimum temperature may be more important than the absolute difference between surface and subsurface water temperatures.

Applying the energy bonus hypothesis to *P. borealis* in the Gulf of Maine, it is possible that shrimp which migrate vertically from colder bottom water into warmer intermediate or surface water to feed at night and return to the bottom and assimilate their food during the day have greater energy reserves to devote to growth and/or egg production. Egg production, expressed as the number of eggs which are deposited at spawning (fecundity), is in turn a consequence of the number of oocytes which are produced in the ovary and the percentage which actually survive to spawning, both of which could be affected by temperature changes encountered during vertical migration.

If the degree of thermal stratification does affect the fecundity of northern shrimp in the Gulf of Maine, one would expect to find more fecund females in the southwestern region of the Gulf, particularly west of Jeffreys Ledge, where thermal stratification develops in the spring and prevails through the summer. There was some evidence that intermediate-sized (but not large or small) shrimp collected east and west of Jeffreys Ledge were more fecund than shrimp from two other locations in the southwest Gulf of Maine in August 1968, but the September results did not show higher fecundities for shrimp collected west of Jeffreys Ledge. If there is, in fact, an effect of temperature change on fecundity, it would have been difficult, if not impossible, to detect in a field study like this one where water temperatures were measured at discrete locations and points in time. Oogenesis has been reported to last from January until May in the Gulf of Alaska (Nunes 1984). If egg numbers are also determined during the fall and/or winter in the Gulf of Maine, vertical differences in temperature could not be invoked as a factor affecting fecundity (since vertical temperature profiles are isothermal or nearly so during that time of year in the Gulf of Maine), unless fecundity is also a function of events which take place after the number of eggs in the ovaries is determined (i.e., factors which might affect the survival rate of oocytes). A field study clearly cannot be expected to answer all of these questions.

Evidence for a relationship between fecundity and temperature is provided by comparing previously reported changes in the mean annual fecundity of 25 mm CL *P. borealis* in the Gulf of Maine between 1962 and 1982 with average annual April-July bottom water temperatures from various locations in the southwestern Gulf of Maine (Fig. 23). Fecundities were high in the mid-1960s, low in the late 1960s and early 1970s, and high again in the late 1970s (Table 7). As a working hypothesis, we propose that the mechanism controlling long-term variations in fecundity and, perhaps, changes in population size, is water temperature, or, more specifically, the magnitude of the temperature difference encountered by maturing female shrimp during diurnal vertical migration. High fecundities in the mid-1960s and late 1970s corresponded with periods of low April-July offshore bottom water temperatures in the southwest Gulf of Maine; low fecundities in the late 1960s and early 1970s corresponded with high offshore bottom water temperatures recorded in the same locations and time of year (Fig. 24). Since vertical migration is apparently impeded by temperatures >6°C (Fig. 12), we suggest that high fecundity is associated with a greater positive differential between 6°C and the observed bottom water temperature, a condition which existed in the late 1960s and late 1970s (Fig. 23). A linear regression of fecundity vs. April-July bottom water temperatures (Fig. 24) showed that a 26% reduction in fecundity was associated with an increase from 4° to 6.25°C in temperature during the period 1973-82. A similar rate of decline in fecundity was observed between 1968 and 1969 when May-July bottom water temperatures were 3.5° and 5°C, respectively (Table 7), although the data shown in Figure 24 suggested that fecundities were lower in 1968 and 1969 than in 1973-82 for other reasons.

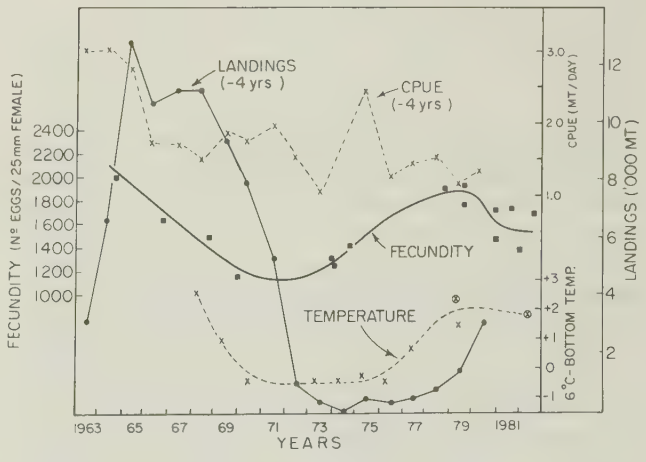


**Figure 23.—Predicted mean fecundity per 25-mm dorsal carapace length female *P. borealis* for selected years during 1964-82; 6° minus mean April-July bottom water temperatures for offshore stations 3-7 (see Table 2 and Figure 4) for selected years 1968-82; annual 1967-82 Gulf of Maine landings; and annual 1967-77 catch-per-unit-effort data. Landings and CPUE data were lagged backwards 4 years to account for the time delay between larval hatching and recruitment. Curves were drawn by eye. *Legend*: *X* = May-July temperatures; (*X*) = April, June temperatures. *Sources*: Fecundity data are from Stickney and Perkins (1981). Temperature data for 1968-79 from Welch and Churchill (1985), and for 1979 and 1982 from Charles Parker, Bigelow Laboratory for Ocean Sciences. Landings and CPUE data are from Diodati et al. (1984).**

**Table 7.—April-July bottom temperature data for the southwestern Gulf of Maine (stations 3-7) expressed as mean bottom temperatures and 6° minus mean bottom temperature, predicted mean fecundities (linear model), total Gulf of Maine landings, and catch-per-unit-effort estimates, 1964-82.**

| Year | Bottom temp. (°C) Mean[a] | 6° − mean | No. eggs/ 24-mm female[b] | Landings ($10^3$ MT) | CPUE (MT/st day)[c] |
|---|---|---|---|---|---|
| 1964 | | | 2,000 | | |
| 1966 | | | 1,645 | | |
| 1968 | 3.5 (16) | 2.5 | 1,471 | 6.61 | 2.99 |
| 1969 | 5.0 (4) | 1.0 | 1,150 | 12.82 | 2.77 |
| 1970 | 6.4 (1) | −0.4 | | 10.67 | 1.67 |
| 1971 | | | | 11.13 | 1.60 |
| 1972 | | | | 11.10 | 1.53 |
| 1973 | 6.4 (2) | −0.4 | 1,270 | 9.40 | 1.83 |
| | | | 1,293 | | |
| 1974 | 6.5 (3) | −0.5 | 1,431 | 7.94 | 1.77 |
| 1975 | 6.2 (8) | −0.2 | | 5.29 | 1.93 |
| 1976 | 6.5 (5) | −0.5 | | 10.22 | 1.46 |
| 1977 | 5.2 (4) | 0.8 | | 0.39 | 1.08 |
| 1978 | | | 1,901 | — | — |
| 1979 | 3.8 (10) | 2.2 | 1,933 | 0.49 | 2.43 |
| | | | 1,772 | | |
| 1980 | | | 1,720 | 0.33 | 1.20 |
| | | | 1,491 | | |
| 1981 | | | 1,750 | 1.07 | 1.44 |
| | | | 1,396 | | |
| 1982 | 4.2 (3) | 1.8 | 1,680 | 1.53 | 1.48 |

[a]Numbers in parentheses are numbers of observations.

[b]Fecundity expressed per 25 mm dorsal CL (= 28.5 lateral CL) during the same year when eggs were spawned (i.e., the same year temperature measurements were made). In some years, fecundities were estimated for more than one sample.

[c]CPUE expressed per 12 hour day for commercial 34-50 GT vessels, using trip data for Gloucester and Portland, for which 50% or more of the total catch consisted of shrimp.

Sources: Temperature data from Maine Dep. Marine Resources (1968-77) and Charles Parker, Bigelow Laboratory for Ocean Sciences (1979 and 1982). Fecundity data for 1964-81 from Stickney and Perkins (1981). Landings and CPUE data from Diodati et al. (1984).

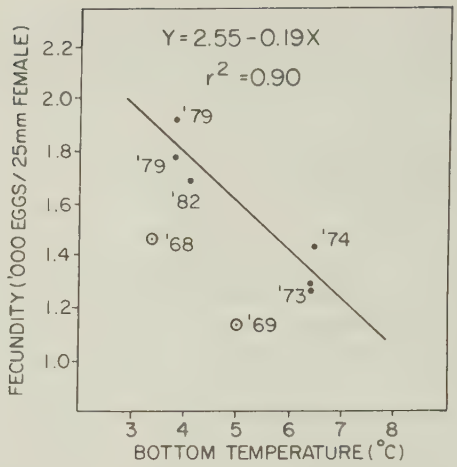


**Figure 24.—Fecundity per 25 mm dorsal carapace length female vs. April-July bottom temperatures in the southwestern Gulf of Maine for the period 1973-82 (1968 and 1969 data not included in linear regression).**

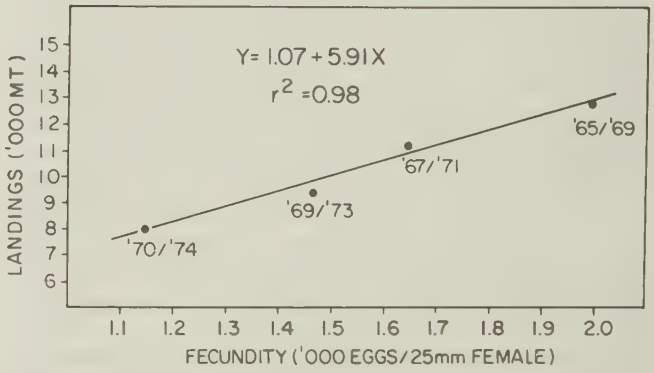


**Figure 25.—Total Gulf of Maine shrimp landings vs. fecundity per 25 mm dorsal carapace length female 4 years earlier for the period 1969-74.**

Support for the hypothesis that water temperature and fecundity are inversely related is provided by a laboratory study by Nunes (1984) of *P. borealis* held at low (2°-3°C), high (8°-9°C), and ambient (annual range of 4°-10°C and mean of 6.3°C) water temperatures for two entire reproductive cycles. Fecundities at low and ambient temperatures were greater than fecundities at the high temperature. After evaluating the effects of temperature on a number of reproductive characteristics (i.e., egg production, embryonic development, egg loss, size of larvae, larval hatching success, and larval viability), Nunes concluded that the optimum temperature range for reproductive success was 3°-6°C and that population fecundity in the Gulf of Alaska could vary with temperature by as much as 20%.

Temperature-induced changes in fecundity could partially explain how population oscillations such as those observed in the Gulf of Maine during the last 30 years were produced. The dramatic decline in landings and CPUE in the early and mid-1970s was preceded by a period of declining fecundity (Fig. 23). In fact, landings during 1969-74 were directly related to fecundities in 1965-70 (Fig. 25), suggesting that diminished egg production per female during 1965-70 reduced the recruitment of 4-year-old shrimp into the exploitable population during 1969-74, thus leading to reduced catches[10]. The fact that such a relationship could be demonstrated is remarkable since: (1) egg production would also depend on the numbers of female shrimp bearing eggs in any given year; (2) recruitment must also be affected by survival rates of eggs, larvae, and 1 to 3-year-old shrimp; and (3) landings are directly proportional to fishing effort which increased by about 1/3 between 1969 and 1974 (Anthony and Clark 1980). Regression analysis of fecundity vs. CPUE and fecundity vs. catch rate data from bottom trawl surveys (Table 7) failed to reveal any relation between fecundity and these two estimates of population size. The increased incidence of lethal egg parasites observed in shrimp exposed to temperatures >5.5°C during the fall inshore spawning migration (Table 5) could be expected to increase egg mortality and also reduce recruitment at age 4.

[10]An additional data point for 1979 landings-1975 fecundity was omitted from the linear regression analysis since 1979 landings were limited by a short season (February 1-March 31) and low fishing effort. High catch-per-unit-effort in 1979 further indicated that landings in that year bore no relation to population size.

## Population fluctuations and management implications

Large, cyclical variations in landings and catch-per-unit-effort over the past 30 years (Figs. 1-3) suggest that the northern shrimp population in the Gulf of Maine undergoes fairly extreme, non-random fluctuations in abundance which we contend are related primarily to temporal changes in seawater temperature. The northern shrimp population in the Gulf of Maine exhibits several biological characteristics of an immature or unstable population as described by Margalef (1963). Among the characteristics he described are the following:

1) "Animals tend to spend their adult lives in the more mature system but to reproduce in the less mature ones and send larvae into them;

2) . . . A unispecific population that expands over a wide range has local differences in demographic structure, even when internal flow of individuals is important;

3) Less mature systems species tend to be opportunistic. . . and. . . are subjected to a dynamic type of selection, often for prolificness;

4) Large fluctuations are to be expected; a rapid increase of numbers is possible only in a system that works with low efficiency;

5) Fluctuations of abundance are heavily influenced by external inputs; i.e., by changes in the physical or abiotic environment."

The following aspects of the life history of *P. borealis* in the Gulf of Maine correspond to the five characteristics of an unstable population listed above:

1) The migratory behavior of this species in the Gulf results in the partitioning of juvenile and adult life stages, with juvenile stages restricted to inshore waters where a more variable annual temperature regime prevails and adult life stages found in thermally more stable offshore waters, a pattern which is modified by the inshore spawning migrations of female shrimp;

2) Despite an inshore-offshore migration, local differences in length frequency distributions are evident;

3) Natural selection for maximum reproductive output in a species which does not produce many eggs per female has resulted in the evolution of sequential hermaphroditism, a process by which the capacity of larger individuals in the population to function as egg-bearers (females) is capitalized;

4) Large fluctuations in catch and stock abundance have been experienced in the fishery, a small one in the 1940s and a much larger one between 1965 and 1975;

5) These fluctuations in abundance correlate fairly well with long-term periodic changes in mean annual sea surface temperature.

Both catch data and biological information therefore suggest that the northern shrimp population in the Gulf of Maine is unstable. The strong correspondence of life history characteristics and migratory behavior with spatial and temporal temperature changes in the Gulf of Maine underscores the importance of Margalef's fifth characteristic: abundance is strongly influenced by the physical environment. We conclude, therefore, that in the Gulf of Maine, at the southernmost extension of its range, the abundance of this boreal species is strongly influenced by environmental factors, and that, by means of its migratory behavior, it has adopted an opportunistic life history strategy that permits it to exploit a favorable condition (cooler water temperature) to the maximum extent. The opposite situation exists along the coast of West Greenland near the northernmost extension of this species range, where periods of warmer bottom water temperatures (above zero as opposed to subzero) have been associated with stable yields (Smidt 1965, 1967). Populations such as this one which undergo large-scale fluctuations in abundance which are influenced primarily by physical features of the environment do not respond well to attempts to control exploitation.

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